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THE ROLE OF THE PREMANDIBULAR OR INTERCALARY SEGMENT IN HEAD SEGMENTATION OF INSECTS AND OTHER ARTHROPODS *

BY F. H. BUTT

Cornell University

The problem of head segmentation of arthropods and especially of insects has long received the attention of entomologists and those interested in other arthropods. Though many celebrated workers have presented their views on this problem over the past 75 years and many others less celebrated have contributed further evidence, the problem has remained unsolved. One of the most remarkable aspects of the work on the head is the uniformity of the observations and illustrations over this period. It is indeed surprising that so many diverse interpretations have arisen based on these observations and illustrations. I hope that my interpretations will help to clarify the problem.

Before progressing further, certain terms must be defined. As defined by Snodgrass (1935) the term "segment" means "a subdivision of the body between areas of flexibility associated with muscle attachments", as for example the segments of the antennae or the leg. In the present study we are not interested in the term "segment" used in this sense. We are considering here, rather a "primary body segment" or "somite" which in the embryo is known as a "metamere." Thus the term "segment" should be defined more fully with consideration of the

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whole development from the early embryonic germ band to the full grown adult. A primary body segment then, is a ring-like portion of the body separated from similar rings by areas of flexibility, and bearing at some time during the development of the animal a pair of appendages which may consist of simple transitory lobes in the embryo. Each segment has early in its development a pair of coelomic sacs; and each has a ganglion forming a part of the central nervous system with nerves running to the appendages.

Head Segmentation: Insecta

The early germ band consists of a thickened area of the blastoderm on the ventral side of the egg, broadly expanded at the anterior end and narrowing posteriorly. Krause (1938) illustrates the embryo of *Tachycines* as heart shaped (fig. 1), and has indicated in his diagram the presumptive areas of the head, thorax, and abdomen. The heart shape is the usual form of the early germ band though some insects vary from this to a considerable degree (figs. 2, 3, 4).

In *Oncopeltus* a slender tube-like invagination pushes into the yolk at the 35th hour (Butt 1949). The wall of this tube nearest the ventral surface of the egg is made up of the germ band; the remainder of the tube is the amnion. This process of invagination continues during the second and third days of development until the embryo reaches its greatest length at the 59th hour when the tail end extends half way back from the anterior pole on the dorsal side of the egg. During this time the head lobes, which cover a considerable portion of the posterior end of the egg, never enter the yolk through the blastopore-like opening but remain on the surface. Later, the head lobes sink into the yolk and are overgrown by the amniotic folds.

Shortly after the embryo reaches its greatest length, transverse grooves appear in the ectoderm. This occurs soon after the inner layer is formed. At 46 hours the embryo is perfectly smooth without metameric grooves; ten hours later metameric grooves appear representing the three thoracic segments. From the thoracic region segmentation spreads forward and backward, but at the very earliest stage (fig. 5) with the exception of two rather indistinct lobes, which I judge to be the mandibles, the

gnathal appendages are not present. The segmental grooves appear and grow very rapidly and at a slightly later stage (fig. 6) the first and second maxillae are well formed. In both of these early stages a pair of faint lobes, widely spaced from each other, appear just within the amniotic cavity with another more distinct pair apparently located posterior tc them. These latter lobes are the antennae; the former are the lobes that will form the labrum.

Up to the stage represented in figure 6, the stomodaeum has not appeared but at approximately the 65th hour a slight indentation forms on the mid line, illustrated in a sagittal section in figure 9. This indentation, the stomodaeum, rapidly deepens (fig. 10). At the 71st hour the relationship of the labrum to the stomodaeum, and the antennae becomes apparent since at this hour the labral lobes have come together to fuse in front of the mouth, and the antennae are now revealed as forming from the inner edges of the head lobes. The bi-lobed nature of the labrum continues to be evident for a considerable length of time before it starts to elongate to form a cover for the mouthparts in the labial trough (fig. 7) at about the hundredth hour.

There are several facts that are evident from this description and from the illustrations referred to so far. First, the stomodaeum does not form on the anterior extremity of the embryo and is never terminal in position. Second, the labral lobes are paired and are widely separated from each other when they first appear. Third, they move in front of the stomodaeum where they fuse to form the upper lip. Finally though the antennae appear to be posterior in position to the labral lobes, they arise from the inner caudal extremities of the procephalic lobes and are thus morphologically anterior to the labral lobes. Other well-known facts concerned with the labrum are, first: that coelomic sacs are present in the region of the labral lobes, and second: these lobes have well-defined nerve connections with the tritocerebral ganglion.

Despite this obvious evidence that the labral lobes represent a pair of appendages belonging to the tritocerebral segment, students have been taught for years that the labrum itself was simply a flap of the cuticula and had no broader significance; the

presence of mesoderm and of nerve connections was just a secondary circumstance.

A search of the literature reveals that over the past 70 years many others have observed the bilobed origin of the labrum in insects. In *Pyrilla* (order Homoptera) according to Sander (1956) the labrum is clearly bilobed and shows two distinct coelomic cavities. Figures 11 and 12 are taken from the work of Blunk (1914) on *Dytiscus*. In the first illustration, the labral lobes are far apart; in the second they are nearly touching. In the Lampyridae the labral lobes appear to be connected one with the other by a darkened area passing beneath the stomodaeum, (figs. 13, 14), a condition that is quite common in the Coleoptera. It may be significant that these two drawings appeared in a work done by Williams (1916) incidental to his study of the light producing organs.

Two years before Blunk published his paper, Korschelt (1912) working with *Dytiscus* described the later development of the labrum. Though it is well formed as an upper lip anterior to the stomodaeum in all four figures from his paper, it still shows evidence of its bi-lobed origin (figs. 15, 16, 17, 18). Korschelt says he could not find any proof of a truly paired origin of the labrum in the available stages of *Dytiscus;* however, if he had had earlier material comparable to Blunk's and Williams' I am sure he would have found this proof as Blunk found for *Dytiscus* and Williams for the Lampyridae.

In Korschelt's figures the labrum is in place above the stomodaeum, and all other gnathal appendages are present behind the stomodaeum. In some beetles, notably *Brachyrhinus* (Butt 1936), at this stage of development not only are there lobes representing appendages present on the gnathal and thoracic areas but each segment of the abdomen except the telson bears a pair of lobes as well. The embryo at this time has reached a stage of development that is equivalent to the adult trilobite and to the trilobite larva of *Limulus;* therefore, this period in the embryonic history of an insect should be known as the "trilobite stage."

According to a paper by Smreczynski (1932) the migration of the labral lobes in *Silpha* occurs in a similar fashion (figs. 19-20-21). A figure of *Acilius* taken from Patten (1888) shows a

similar condition to Williams' lampyrid figure made many years later (fig. 22).

Perhaps the most complete series we have illustrating the development of the labrum is found in Tiegs and Murry (1938) on *Calandra*. Figures 23 to 26 illustrate the early embryo from the time segmentation starts to the time when the labral lobes put in their appearance. In *Oncopeltus* they appeared early in the process of segmentation; in *Calandra* their appearance is delayed considerably. Figures 27 to 29 illustrate the further migration of the head lobes onto the dorsal side, the fusion of the labral lobes to form the labrum, and the migration of the labrum to the extreme anterior point of the egg.

In the Lepidoptera the bilobed origin of the labrum is shown very well by Johannsen (1929) and in a paper by Rutschky and Presser to be published during the coming year. The egg of *Heliothis obsoleta* as described in the latter work, is cylindrical and somewhat flattened dorsoventrally. This causes the embryo to roll up in a rather tight, somewhat spiral coil as indicated in figures 30, 31, 32, with the head partially covered by the tail and upside down. Figures 33, 34, 35 show the head in this inverted position with the anterior edge of the head lobes on the lower side. The labral lobes are widely separated at first (fig. 33) but as development proceeds, they move closer together (fig. 34) and finally fuse (fig. 35). In later stages the labrum appears at the extreme anterior end of the embryo because of the bending backward of the head lobes, and for a long time traces of its bilobed origin may be seen (figs. 36, 37, 38). A similar origin for the labrum in *Mamestra configurata* is indicated in figure 39 (Rempel, 1951).

These figures presented in this paper are by no means a complete study of the literature on embryology but represent those papers in which the bilobed origin of the labrum is most obvious and is best illustrated. Now the question arises—how does the labrum form in other arthropods?

Head Segmentation: Other Arthropods

Figures of the early germ band of *Latrodectus mactans*, the black widow spider (figs. 41, 42) show a remarkable similarity in development to that of the insect. In the spider a pair of

lobes appear near the anterior end of the embryo after the lobes representing the chelicerae, the pedipalps, and the four pairs of legs have already formed (fig. 41). These lobes at the anterior end of the germ band soon come together, fuse and take their position, forming a single lobe in front of the stomodaeum (fig. 42). This is the rostrum (lr) and corresponds to the labrum of insects. This sequence of events has recently been observed by Rempel and will soon be published. Kastner (1949) indicates a similar development for the rostrum in *Thellyphonus caudatus* (Pedipalpi) (figs. 44, 45, 46, 47). Concerning these observations two points should be noted: the remarkable parallel development of the rostrum with the development of the labrum in the insects, and the remarkable clarity of the drawings representing the early stages of development of the head.

According to Lambert (1909) who described the procephalic lobes of *Epiera cinerea,* Schimkewitch was able to demonstrate in 1887, that the rostrum in spiders arises as a pair of prominences on the anterior margin of the cephalic plate, these prominences uniting later to form the upper lip. And again later in the same paper he points out that Schimkewitch considered that these prominences, by their structure, represent a pair of cephalic appendages. In reference to his own work Lambert says that in sections these elevations are seen to be lined with mesoderm and enclose a portion of the coelomic cavity, a fact which indicates their appendage-like character. Figure 48 taken from Lambert's paper of 1909 corresponds very closely with figure 41 taken from Dr. Rempel's work now in press.

In both the insects and the spiders the appendages of the labral segment never develop beyond the most rudimentary lobe-like stage, but in the Crustacea a pair of well-formed appendages, the second antennae, develop from this segment and only the basal triangular area of the appendages fuse to form the labrum proper. The figures illustrating this development were taken from a paper by Sollaud (1923) on the embryogeny of the Palaemoninae.

In this animal, cells of the blastoderm group themselves into two strips on the ventral side of the egg. These strips converge and join at the germ disc (fig. 49). When the strips become

segmented, the lobes are designated by Solland as the ophthalmis, first antennal, second antennal, and mandibular lobes (fig. 50). As these two strips converge, the embryo begins to take on the familiar appearance of the nauplius form (fig. 51). The stomodaeum (fig. 52) appears at the posterior border of the first antennal segment. As the first antennae fuse more completely with the ophthalmic lobes to form what in the insects is called the procephalon, the second antennae begin to form as biramous appendages with median basal areas located near the stomodaeum (figs. 52 and 53). Next we see a median labrum located over the mouth opening but with distal biramous appendages still present (fig. 54). Would it not be logical to assume that the labrum represents the fused basal areas of the second antennae shown in the previous figure? Figure 55 represents later stages in development showing the mandibles, the first and second maxillae and the maxillipeds.

Now let us consider an arthropod that never develops these labral lobes or second antennae. I refer to *Pauropus* of the Myriopoda; the illustrations used here were taken from a paper by Tiegs published in 1947.

Since intersegmental lines are suppressed in *Pauropus* until an advanced stage of development, the chief external guide to the segments, according to Tiegs, " must therefore be the appendages and the ventral organs." The ventral organs do not protrude beyond the surface of the head but are recognizable by the peculiar radiating orientation of their nuclei and can be seen in stained whole embryos. They are present in the " pre-mandibular ", mandibular, and the maxillary segments at a stage represented by figure 59.

By the sixth day the antennae have begun to form as " gentle swellings " on the surface, to use Tieg's expression, not as pronounced lobes as in insects I have discussed so far. The antennae at first lie postorally (fig. 56) and as they move forward they give the impression—" that a post-oral antennary segment is in process of curving forward round the stomodaeal opening." Again Tieg's words.

The mandibles and maxillae soon form, again as " gentle swellings." The pre-mandibular area on the other hand does not

exhibit these swellings. All three of these segments bear ventral organs which afford us the opportunity to trace the forward migration of the gnathal segments.

As this movement proceeds, the ventral organs of the premandibular segment move to the corners of the stomodaeal slit where they migrate onto the under surface of the labrum now beginning to cover the mouth opening. They thus take their position on the epipharyngeal surface of the labrum.

"This epidermis", says Tiegs in reference to the pre-mandibular segment, "later plays a large part in the formation of the clypeus, and it is therefore evident that, as in the Symphyla, this part of the head-capsule must be largely of pre-mandibular origin. (Both in insects and myriopods the innervation of the clypeus and labrum from the tritocerebrum has long been known.)"

As the labrum grows down over the stomodaeum, and the mandibles and maxillae group themselves around it, the mouth sinks deep into the head and there is formed in front of it the pre-oral cavity.

Now Tiegs consistently calls the upper lip "the clypeus" which might possibly indicate that he felt that since the labral lobes are not present in *Pauropus* he was not justified in calling the upper lip the labrum. But all the appendages are so flattened that they can hardly be said to form as true lobe-like appendages. An examination of Tiegs' figures indicates that there is a remarkable similarity between the mandibles, maxillae and the median upper lip. I think, therefore, that the term "labrum" is more correctly applied to the upper lip, than "Clypeus."

Cephalization

The evidence of these papers indicates that the labrum is made up of fused lobe-like appendages that migrate around the mouth and come to form the upper lip. Other evidence that indicates that they are true appendages is the presence of coelomic sacs in the head and their connection with the central nervous system, which will be touched upon later.

The fact that these lobes when they first become distinct are located close to the anterior border of the head lobes has led some workers into the erroneous belief that they are appendages of the " first segment of the head." By this I assume they mean of the protocerebrum. But the nerve connections of these lobes are with the tritocerebral lobe of the brain which is formed in the embryo as the first post-oral ganglion.

In the honey bee between the 44th and 46th hours, stage VIII, of Nelson (1915), the entire germ band has reached such a length that the procephalic lobes curve around the anterior pole and lie on the dorsal side with their anterior ends directed caudad. In the anterior region the three lobes of the brain can at this point be made out, the tritocerebral lobes being in line with the posterior border of the stomodaeum. Thus Nelson says, " They are in fact nothing more or less than the much discussed ' second antennae ' of Bütschli and the transitory anterior appendage of Grassi." A section transverse to the long axis of the egg and passing through these three pairs of lobes appears in figure 62 taken from Nelson's figure 52. This drawing represents the ectoderm of the procephalic lobes before the brain has begun to form. The next figure corresponding to Nelson's figure 55 shows the same areas with the tritocerebrum already separated from the ectoderm but with the deuto- and protocerebrum still connected with the ectoderm (fig. 63). At this time the suboesophageal commissure can be seen forming a connection between the lobes of the tritocerebrum. Figure 64 (same as Nelson's figure 56) shows this process practically completed. Already the forward migration of the tritocerebrum can be noticed. Figure 65 illustrates the anterior end of the central nervous system indicating the curvature of the brain so that the anterior lobes (Br) actually lie behind the deutocerebrum and the tritocerebrum.

Lateral external views of the larval head also illustrate that the actual position of the head lobes comes to be posterior to the front of the insect where the labrum is located in the honeybee (Nelson 1915, Schnetter 1934) and in *Pimpla turionella* (Bronskill, unpublished ms.)

The movement of the tritocerebral lobes in a forward direction and the migration of the labral segment around the mouth

simply represent the instigation of cephalization, a phenomenon that occurs universally in the embryonic period of insects and some other arthropods. After an interval of time the mandibles and maxillae follow the labral lobes forward, and as Tiegs has so well described the process in Pauropoda, they group themselves around the mouth to form the ingestive apparatus of the larva. But this is not the end of cephalization. In some beetles, such as the scarabeids, the ganglia continue their forward migration until they are all located in the thorax forming a compact ganglionic mass.

In the spiders this forward movement is accomplished in a somewhat different fashion though the early stages of the embryo could easily be mistaken for many insect embryos. The rostral lobes form the rostrum or labrum in the usual way but as the chelicerae migrate forward they take a position anterior to the rostrum which becomes entirely hidden in the adult spider.

The chelicerae of spiders have been identified as representing the antennae or by some as the appendages of the tritocerebral lobe. I agree with Dr. Rempel that these organs are homologues of the biting jaws of other arthropods and thus are mandibular rather than antennal.

According to Hanstrom (1928) the deutocerebrum and the antennae are entirely wanting in the spiders. Therefore, the brain consists of the protocerebral lobes, the tritocerebral lobes or their vestiges, and the cheliceral ganglion which thus represents the fourth lobe. With the migration of the chelicerae around the mouth the tritocerebral lobes lose their substomodaeal commissures, and become reduced to form the stomodaeal bridge. It is from this bridge that the median stomatogastric nerve, and laterally the two labral nerves, are given off.

In the mites according to Hanström this process of cephalization is carried forward still another step. The 4th pair of lobes migrate still further forward and their post oral connective becomes indistinct or actually lost, though Hanström says it must be present at least in the embryo. The lobes of the 5th segment now move up to take their place laterad of the mouth opening.

In *Limulus* (Hanström 1928), the horse shoe crab, this process has been carried much further. The deutocerebrum is missing

but the stomodaeal bridge is present (3, fig. 72). The stage that corresponds to the trilobite stage of the insect embryo exists in the trilobite stage of the larva. Segment four representing the chelicerae has moved forward but with the connective still arranged post orally. In the adult (fig. 73) the stomodaeal bridge (3) is present. Segment four has moved anterior to the mouth, but so has segment five, and six is more than half way around. Hanström considers the suboesophageal commissure to belong to the chelicerae but if one follows the series as illustrated in figures 66 to 71, should not this commissure belong to the fifth segment?

Figure 66 labelled the "pre-Pauropoda" requires further explanation at this point. Tiegs, as already quoted, says that "the impression obtained from Pauropoda is that a post oral antennary segment is in process of curving forward around the stomodaeal opening." This is contrary to Hanström who thinks that the deutocerebrum never has had a post oral position. But let us suppose that Tiegs' impression is correct. Sometime in the past the ancestors of the Pauropoda had a nerve cord consisting of the protocerebrum and a number of post oral ganglia starting with the deutocerebral ganglion. Then the deutocerebrum migrated around the stomodaeum and lost its post stomodaeal commissure when the tritocerebral ganglion (3, fig. 66) migrated forward to produce the nerve cord of the Pauropoda-Insecta. This process of cephalization has continued through the spiders and the mites to reach its highest degree of specialization in *Limulus* where the fifth ganglion has migrated forward and the sixth is on its way forward.

Using the animal forms discussed, I have prepared two tables to sum up the information presented so far. These tables present the homologies of structures and appendages, with their ganglionic innervations, as understood by earlier workers and of the homologies as interpreted in the light of the evidence presented in this paper.

The first chart gives the comparison with the usually accepted interpretations. For example, the chelicera of the spiders and the mites are presented as homologous with the second antenna of the Crustacea, and with the imaginary intercalary appendages of the insects and the pauropods; the pedipalp

Ganglia of Nerve Cord	Crustacea	Insecta	Pauropoda	Spiders	Mites
Proto-cerebrum	eyes	eyes	eyes	eyes	eyes
Deuto-	antennd 1	antenna	antenna	—	—
Trito-	anntenna2	intercal.	intercal.	chelicera	chelicera
Mandible	md.	md.	md.	pedipalp	pedipalp
Maxilla	mx 1.	mx.	mx.	leg 1	leg 1
Labium	mx 2	labium	labium? (collum)	leg 2	leg 2
Proth.	mxpd.	leg 1	leg 1	leg 3	leg 3
Mesoth.	mxpd 2	leg 2	leg 2	leg 4	leg 4
Metath.	mxpd 3	leg 3	leg 3	—	—

Chart 1.

as homologous with the mandible. This interpretation makes the fourth leg of the spiders and mites homologous with the second leg of the insects and pauropods and with the second maxilliped of the Crustacea. But the first abdominal segment of the spiders and mites has no appendages at any time and it is difficult to interpret this segment as being the equivalent of the segment bearing the third maxilliped of the Crustacea and the third segment of the thorax of the insects and the pauropods.

The second chart, presenting similar comparison between the same animals but with *Limulus* added, incorporates changes in homologies suggested by this paper. Thus the rostrum of spiders, mites, and *Limulus* corresponds to the labrum and the second antenna of the other forms; the chelicera of the last three with the mandibles of the first three; and the pedipalps of the spider and mites and the first leg of *Limulus*, with the maxilla of the others. This makes the fourth leg of the spiders and the mites, and the fifth leg of *Limulus* correspond to the third leg and the third maxilliped of the first three animals in the chart. This seems to be a much more logical grouping and in light of the evidence that the labrum really represents the

Ganglia of Nerve Cord	Crustacea	Insecta	Pauropoda	Spiders	Mites	Limulus
Proto-cerebrum	eyes	eyes	eyes	eyes	eyes	
Deuto-	antenna 1	antenna	antenna	—	—	—
Trito-	ant. 2	labrum	labrum	rostrum	rostrum	rostrum
Mandible	md.	1 md.	md.	chelicera	chelicera	chelicera
Maxilla	mx.	mx.	mx.	pedipalps	pedipalps	1st leg
Labium	mx. 2	labium	labium? (collum)	1st leg	1st leg	2nd leg
Proth.	mxpd. 1	1st leg	1st leg	2nd leg	2nd leg	3rd leg
Mesoth.	mxpd. 2	2nd leg	2nd leg	3rd leg	3rd leg	4th leg
Metath.	mxpd. 3.	3rd leg	3rd leg	4th leg	4th leg	5th leg

Chart 2.

fused appendages of the old intercalary segment, it is more acceptable than the old grouping.

Evidence from Experimental Embryology

The evidence so far presented for these homologies has been taken from descriptive embryological studies and of course is entirely circumstantial. Without some new evidence concerning the origin of the labrum and the course of cephalization, it seems very improbable that entomologists will ever agree on this problem of head segmentation. The greatest hope for new evidence, in fact I believe the only hope, lies in the work of the experimental embryologist.

A recent paper by Haget (1955) on experiments concerning the evidence for the paired origin of the labrum in the embryo of the coleopteran *Leptinotarsa* proves conclusively, it seems to me, that the labrum originates from widely spaced lobes which come together to form the upper lip. At a stage in development before the labrum is formed he destroyed the area of the ectoderm (fig. 74) in the region where the upper lip would be expected to appear; nevertheless, the labrum formed in a normal manner. Further experiments were made in which the ectoderm laterad of this point first on one side only (fig. 75), later on both sides was destroyed (fig. 76). In these embryos, the labrum was only half formed on that side which had not been cauterized, and in the latter experiment no labrum was formed at all.

Schnetter (1934) presents an anlagen plan of the early blastoderm stage of the bee, but it is Seidel (1935) who has published what Richards and Miller (1937) describe as "the only satisfactory worked-out anlagen plan of any indeterminate or incompletely determinate type of insect egg. . . ." In his work he presents the blastoderm plan for *Platycnemis* (Odonata), which indicates the presumptive organ areas even before the embryonic rudiment is formed. In this plan the blastoderm stage is remarkably like that of the embryo after segmentation has set in. Even at this time the antennae are formed at the posterior edge of the head lobes and the area of the intercalary or labral segment or as he calls it, "the supra oesophageal ganglion" surrounds the mouth opening. Unfortunately the island of material which he labels the "labrum" appears incorrectly interpreted if we are to accept Haget's evidence and I think it should be considered the anlagen of the stomodaeum. I mention his plan here because of the fact that it is so clearly an arrangement that is closely duplicated in the embryo at a much later stage of development.

Seidel's method was to produce irradiation defects on the blastoderm as an aid in making these organ anlagen plans. It is apparent that the effect of the defects themselves might have an adverse influence on the development of the embryo. In a recent paper, Ake Holm (1952) has described a method of marking the embryo of the spider with stains in such a way that in-

juries were greatly reduced. Consequently, markings could then be traced, as the material of the blastoderm or the germ band moved or flowed during the process of development. Though his work had no bearing on the formation of the labrum and the labral segment, I mention it here because it seems to be a technique that could be applied in such a study.

Conclusions

In conclusion the evidence presented in this paper indicates that the head lobes arise as broad anterior areas of the germ band and maintain their position throughout embryonic life. These lobes include the protocerebrum and the deutocerebrum in insects and correspond to the acron of the annelids.

The tritocerebral lobes form in the anterior trunk segment and migrate around the stomodaeum to fuse with the brain. The appendage lobes of this segment of the tritocerebrum are the labral lobes. These lobes form from material that moves around the stomodaeum where they fuse to form the upper lip. The anterior movement of the materials, along the mid-line, of the gnathal region during the process of cephalization, in particular the movement of the premandibular area, is all important in the determination of the segments of the head. The mandibles, maxillae, and labium form in the gnathal region, migrate forward, and group around the mouth opening, and the preoral cavity is formed anterior to the stomodaeum between them. The ganglia of these segments move forward to form the sub-oesophageal ganglion. In some forms the ganglia of the thorax and abdomen continue this forward movement to form a single large ganglionic mass in the thoracic region. Thus cephalization starts very early in the embryo with the labrum, and continues after a slight delay with the migration of the other gnathal segments.

As a result of this study, the head of insects appears to be made up of the acron, and the labral, mandibular, maxillary and labial segments.

Abbreviations

ant	—	antenna
br	—	brain
chl	—	chelicera
col s	—	collum segment
cor all	—	corpus allatum
ft gng	—	frontal ganglion
hl	—	head lobe
lb	—	labium
lr	—	labrum
lr nv	—	labral nerve
md	—	mandible
mes	—	mesoderm
mx	—	maxilla
mx pd	—	maxilliped
opt	—	optic lobe of brain
opth	—	opthalmus (lobe of brain)
o schl	—	Oberschlundganglien (of Seidel)
pdp	—	pedipalp
phy gng	—	pharyngeal ganglion
pro th	—	prothoracic leg
ros	—	rostrum (labrum)
soe com	—	suboesophageal commisure
soe gng	—	suboesophageal ganglion
st cleft	—	sternal cleft
stom	—	stomodaeum
vo c	—	ventral organ of collum segment
vo md	—	ventral organ of mandibular segment
vo mx	—	ventral organ of maxillary segment
vo pm	—	ventral organ of premandibular segment

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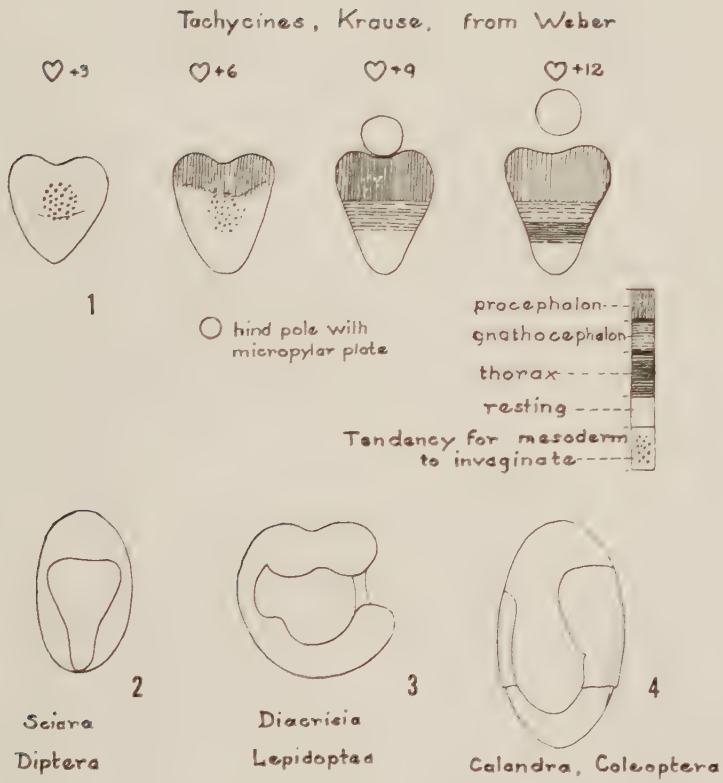
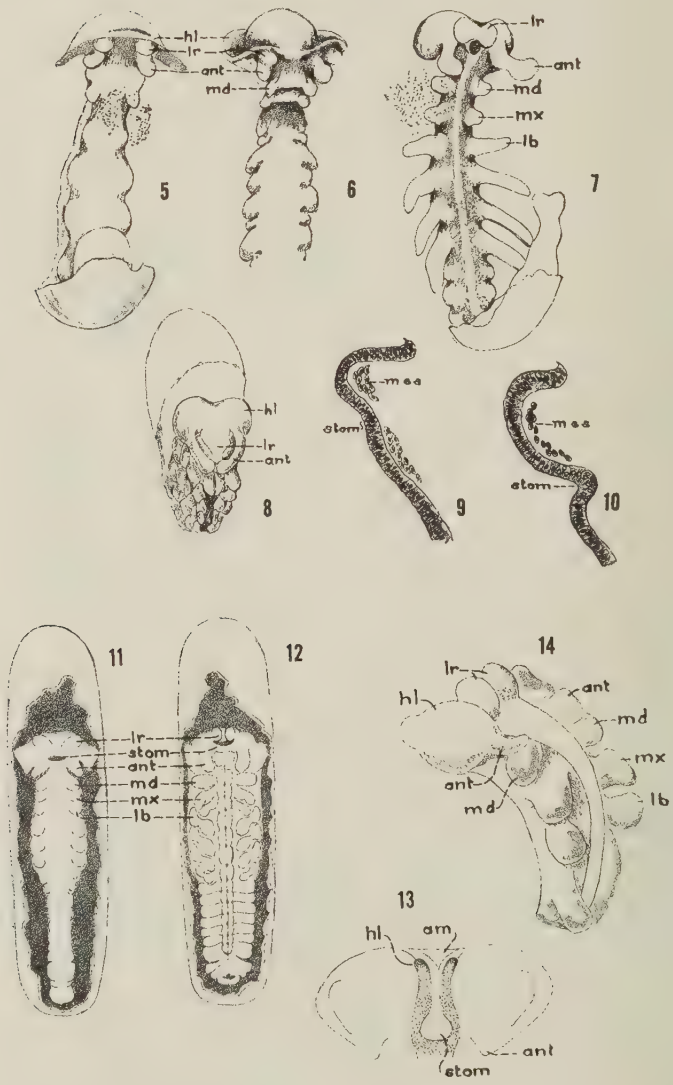
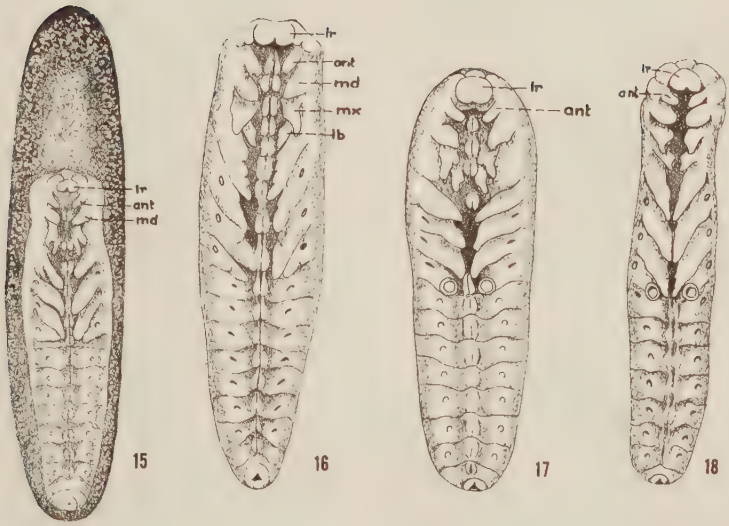


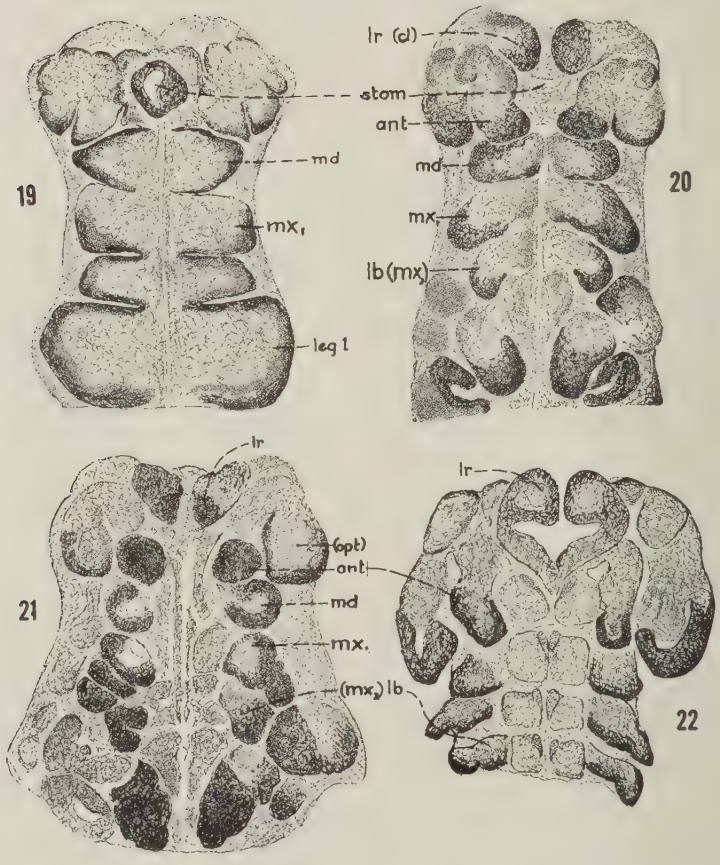
Fig. 1. Early stages of *Tachycines*, from Krause; fig. 2. Early germ band of *Sciara*, Butt 1936; fig. 3. Early germ band of *Diacrisia*, Johannsen 1929; fig. 4. Early germ band of *Calandra*, Tiegs.



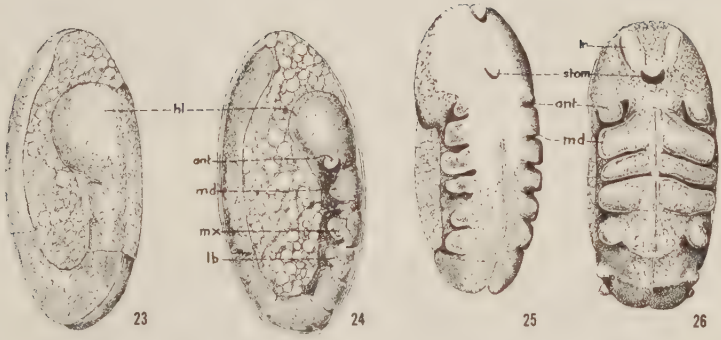
Figs. 5-8. Embryo of *Oncopeltus* during early segmentation and blacktokinesis, Butt; figs. 9, 10. Embryo of *Oncopeltus*, formation of stomodaeum, Butt; figs. 11, 12. Embryo of *Dytiscus* during formation of labrum, Blunk 1914; figs. 13, 14. Embryo of Lampyridae during formation of labrum, Williams 1916.



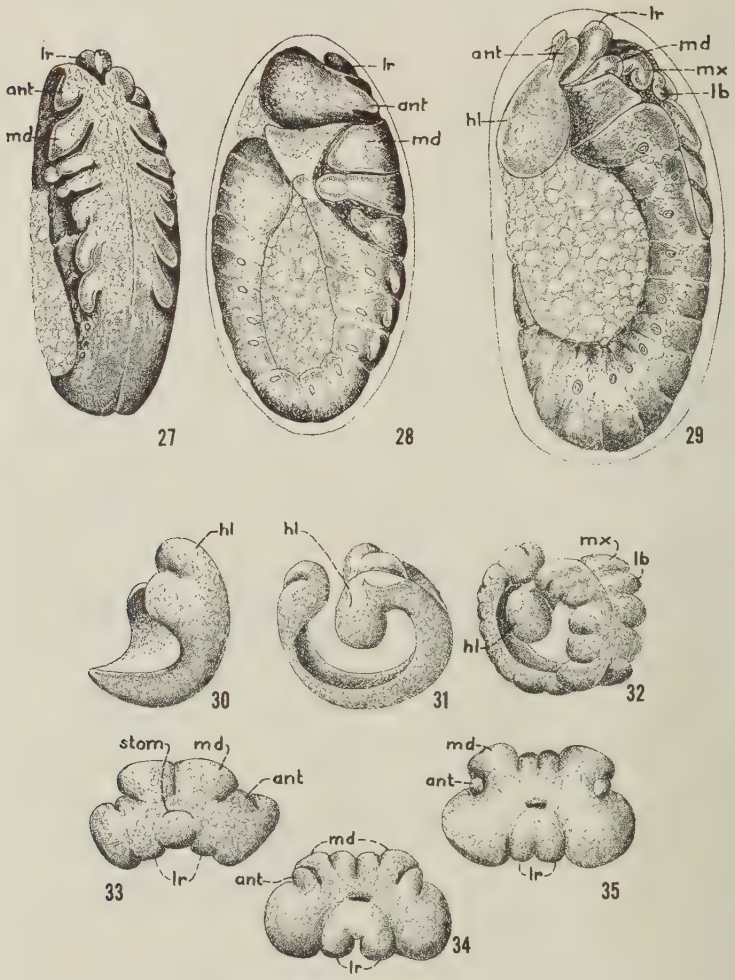
Figs. 15-17. Embryo of *Dytiscus* during later stages of labrum formation, Korschelt 1912; fig. 18. Embryo of *Dytiscus*, trilobite stage, Korschelt 1912.



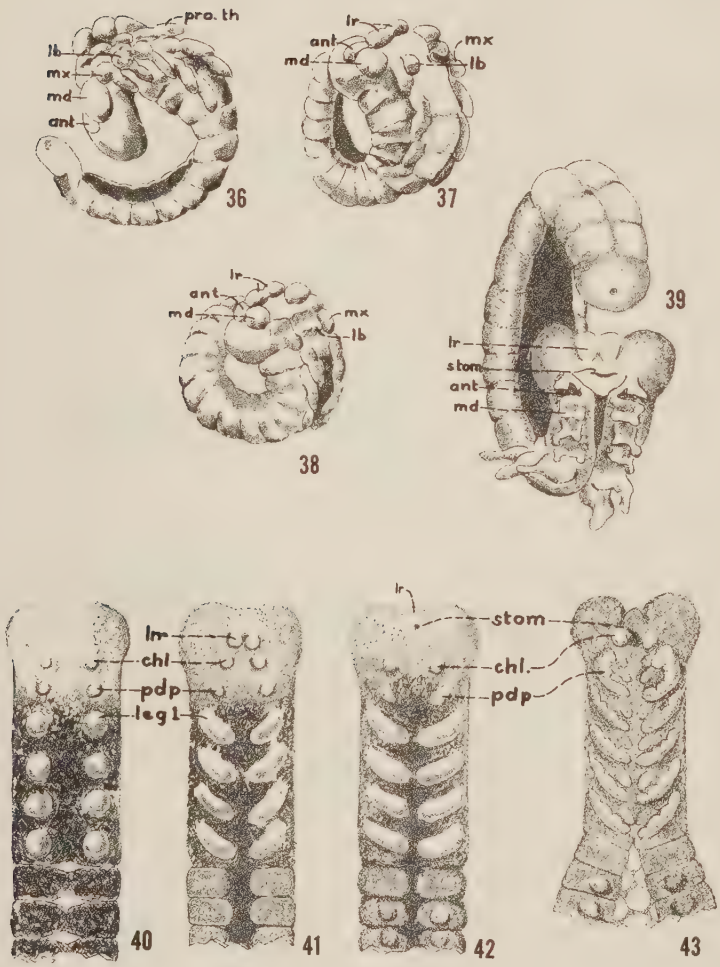
Figs. 19, 20, 21. Embryo of *Silpha* during formation of labrum, Smreczynski 1932; fig. 22. Embryo of *Acilius*, bilobed condition of the labrum, Patten 1886.



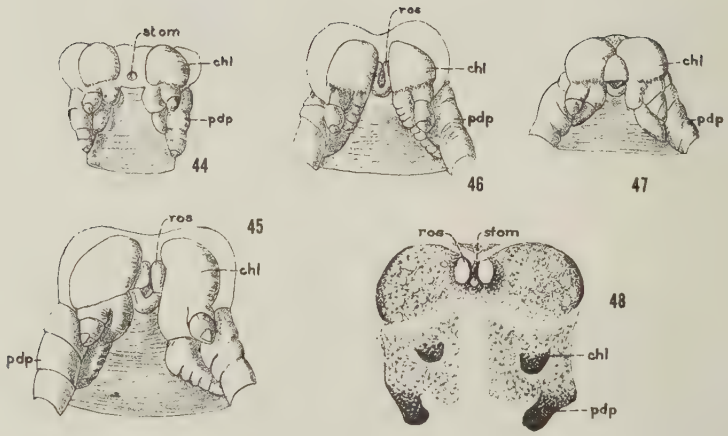
Figs. 23-26. Embryo of *Calandra* during segmentation and growth of labrum, Tiegs and Murry 1938.



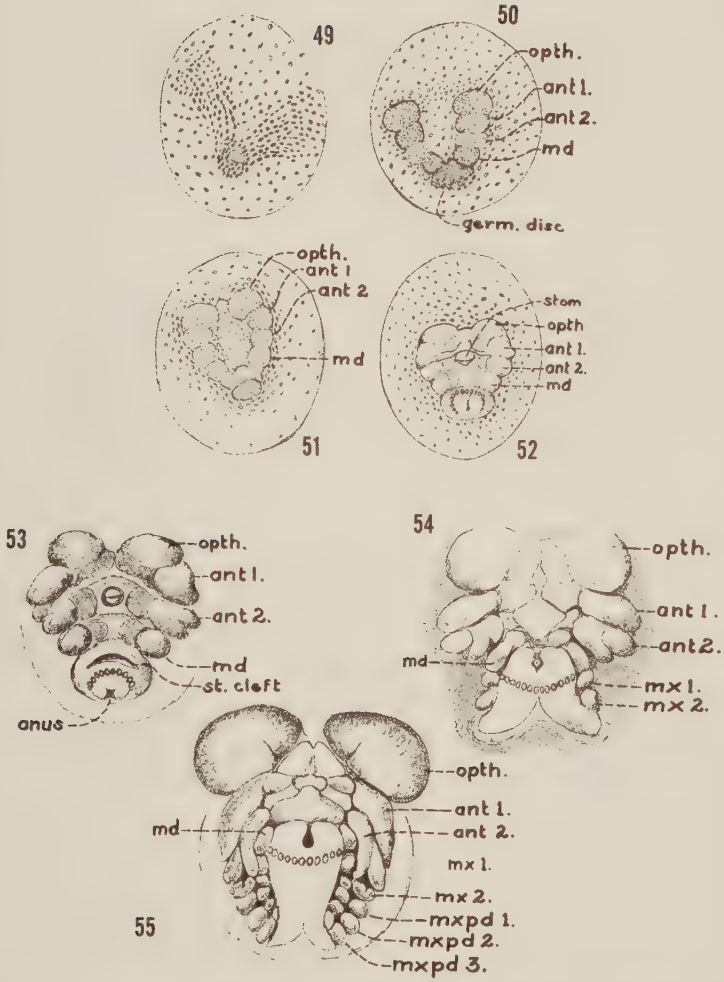
Figs. 27-29. Embryo of *Calandra* during segmentation and growth of labrum, Tiegs and Murry 1938; figs. 30-35. Embryo of *Heliothis obsoleta* during formation of labral lobes, Rutschky & Presser 1957.



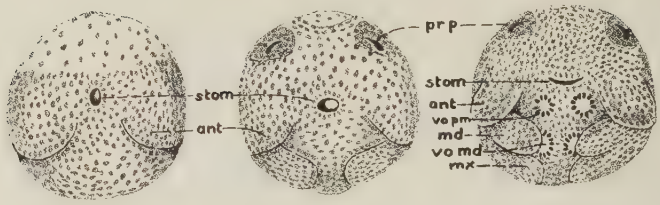
Figs. 36, 37, 38. Embryo of *Heliothis obsoleta* later stages of labrum fromation, Rutschky & Presser 1957; fig. 39. Embryo of *Mamestra configurata* showing bilobed labrum, Rempel 1951; figs. 40-43. Embryo of *Lactrodectus mactans*, the Black widow spider, during formation of rostrum, Rempel 1957, unpublished ms.

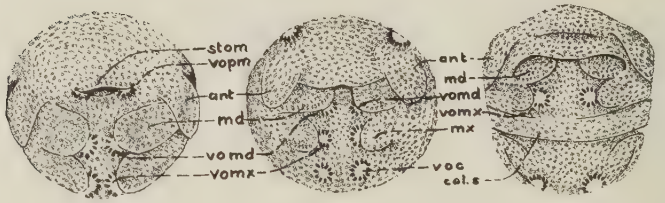


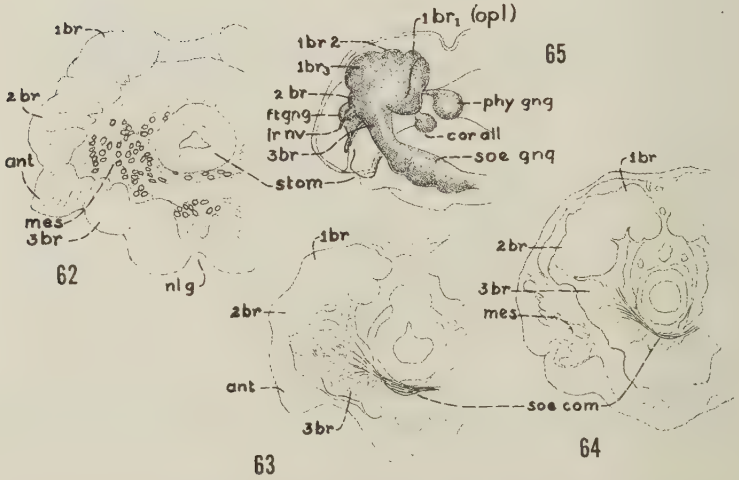
Figs. 44-47. Embryo of *Thellyphonus caudatus* (Pedipalpi), Kastner 1949; fig. 48. Embryo of *Epiera cinerea*, Lambert 1909.



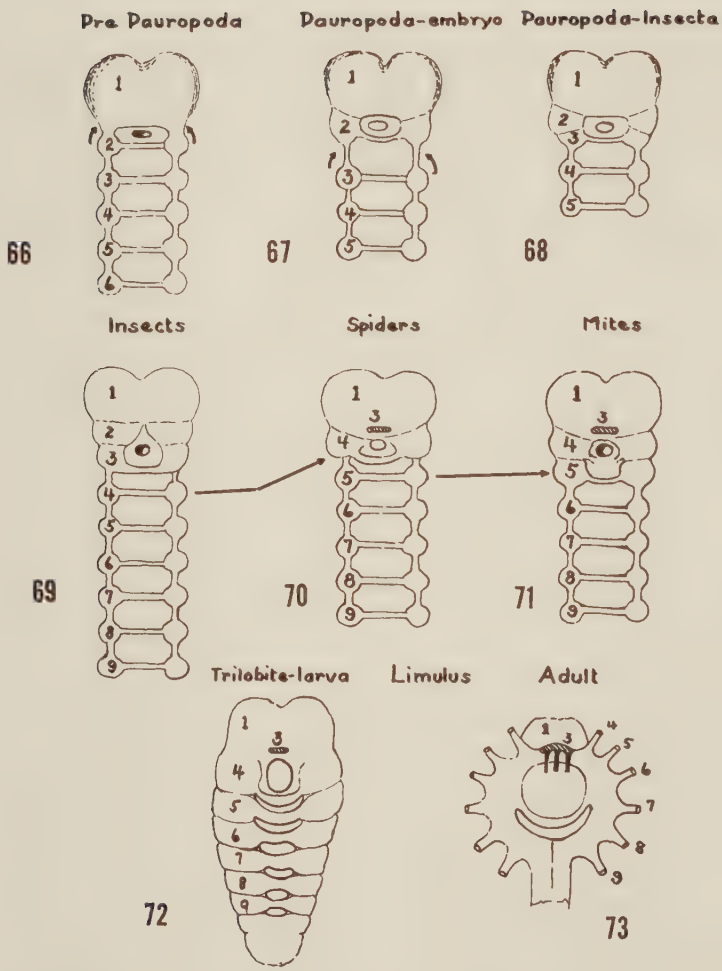
Figs. 49-50. Early germ band of a crustacean Palaemoninae, Sollaud 1923; fig. 51. The nauplius stage; fig. 52. Later nauplius stage; figs. 53-55. Later stages in development of Palaemoninae.



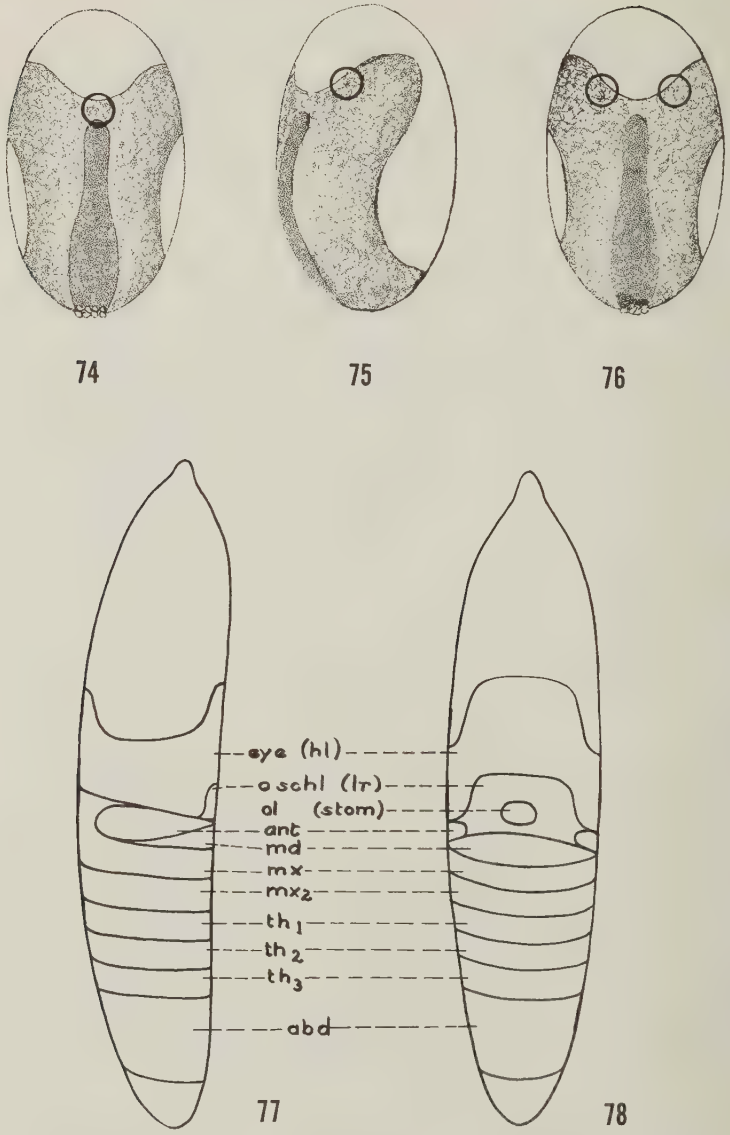




Figs. 56-61. Stages in development of *Pauropus*, Tiegs 1947; figs. 62-64. Development of the brain in cross section, honeybee, Nelson 1915; fig. 65. Lateral view of brain and suboesophageal ganglion of honeybee embryo.



Figs. 66-73. Diagrams of central nervous system to indicate extent of cephalization in the arthropods, adapted from Hanstrom 1928.



Figs. 74-76. Diagrams of the embryo of *Leptinotarsa* to indicate areas of cauterization in the head, Haget 1955. Figs. 77, 78. Plan of the presumptive anlagen for the blastoderm of *Platycnemis*, Seidel 1935.

OBSERVATIONS ON THE BIOLOGY *OF ECTOBIUS PALLIDUS* (OLIVIER) (BLATTARIA, BLATTIDAE)

BY LOUIS M. ROTH AND EDWIN R. WILLIS

Pioneering Research Division, U. S. Army Quartermaster Research and Development Center, Natick, Massachusetts

Ectobius pallidus,[1] the spotted Mediterranean roach, was first collected in the United States in East Falmouth, Massachusetts, in 1948 (Flint, 1951); it has since been reported from other coastal localities in Massachusetts: Falmouth, Manomet, and Plymouth (Gurney, 1953), and Cotuit where two specimens were taken in a house (Gurney, personal communication). In 1955 we collected several male specimens in Natick and one male in Sherborn, Massachusetts, which would indicate that this species is spreading inland. The establishment of this cockroach in Massachusetts probably resulted from an accidental introduction from Western Europe or the Mediterranean area (Gurney, 1953). *E. pallidus* is a nondomiciliary species that occasionally invades houses.

On November 8, 1954, Mr. Paul Rolander collected some oöthecae of *E. pallidus* for us in Plymouth. On this date adults had apparently already died, and he found only a few small nymphs in addition to the egg cases. Rolander (unpublished data) had obtained hatching of eggs from oöthecae only after they had swelled on absorbing water. Following his suggestion, we placed the oöthecae on moist filter paper in our laboratory. On November 24, 1954, some of the oöthecae began to increase in size and to change color. The original color of the hardened egg case was dark brown; this gradually changed to a milk-chocolate

[1] This species has been referred to as *Ectobius lividus* (Fab.) by Flint (1951), and *Ectobius livens* (Turton) by Ramme (1951), Gurney (1953), and Roth and Willis (1955). However, Dr. Ashley B. Gurney, after correspondence with Dr. K. Princis, has informed us that it seems advisable to call this introduced species *Ectobius pallidus* (Olivier).

color after the oötheca had absorbed water and swelled (figs. 1-3). These eggs began to hatch on December 3, 1954. We were unable to establish a laboratory colony from this material.

The following summer we collected large numbers of *Ectobius pallidus* on several trips to Plymouth. On July 12, 1955, adult males and females were numerous under leaf litter in shaded woods. Small nymphs and a few large ones were present but no oöthecae, other than empty egg cases, were found. No females carrying oöthecae were collected on this day, but the following day the females that had been brought into the laboratory began to form oöthecae. On July 19, 1955, we made another collecting trip to Plymouth, and of 157 adult females obtained, 19 were found to be carrying oöthecae. Ovipositing females usually deposited their oöthecae in the laboratory the day following oöthecal formation. The oötheca is formed with the keel upwards and is then rotated so that the seam is directed to the right side of the insect (fig. 13). In the laboratory, complete formation of the oötheca took about one day and rotation occurred about two hours later. Although Rolander (in Roth and Willis, 1955) had claimed that *E. pallidus* carries her oötheca up to 16 days or longer before she deposits it, we found in the laboratory that the females formed and deposited their oöthecae in one to two days; most of the oöthecae were deposited on the moist cotton stoppers of the drinking water vials. Since it was obvious that the eggs had to absorb water before hatching, we kept many of the oöthecae on moist cotton for several weeks. However, these oöthecae did not swell and none of the eggs hatched.

Very few eggs of *Ectobius pallidus* that were deposited in the laboratory hatched. The only ones that did hatch were in oöthecae that had been removed from the moist cotton stoppers, stored dry for about six months, and then allowed to absorb moisture. Oöthecae that were deposited from August 19 to 22, 1955, were stored dry at 23° C. and 50 to 60% R.H. until February 14, 1956, when they were placed on wet filter paper. After they had been kept moist for one to two weeks, some of the oöthecae began to swell. Between March 21 and 26, eggs from six oöthecae hatched; the mean number of offspring per oötheca was 14 (range 13 to 15, N = 5).

When the eggs hatched, the oötheca split along the keel and practically all embryos emerged simultaneously (figs. 4-6). Immediately after wriggling free from the oötheca, the young pronymphs were still enveloped by their embryonic membranes (figs. 7-8), but these were quickly shed (figs. 9-10). Brown (1952) reported similar hatching behavior in *Ectobius panzeri* Stephens.

Eggs of *Ectobius pallidus* apparently must pass through a dormant period or diapause before they will absorb water and complete development. This is indicated by (1) the failure of eggs to hatch when the oöthecae were kept continuously moist from the time they were dropped by the female, (2) the swelling and hatching of field-collected eggs after the oöthecae had been placed on moist filter paper in the laboratory, and (3) similar swelling and hatching of eggs that had been subjected to dry storage conditions for six months before being allowed to absorb moisture. Brown (1952) reported that oöthecae of *Ectobius panzeri* that were produced in the laboratory, as well as those collected on the dunes in the fall, did not hatch until the following spring.

We have similarly observed that the oöthecae of *Cariblatta lutea minima* Hebard also increase in size and change color after being kept on moist filter paper. The eggs of this species do not hatch unless they are kept moist (Roth and Willis, 1954), but, unlike the eggs of *Ectobius pallidus*, the eggs of *Cariblatta* do not undergo a dormant period. The average time for development of *Cariblatta* eggs, when the oöthecae were kept on moist cotton at 27° C., was 26 days (range 23 to 27 days, N = 8).

Apparently in Massachusetts, *Ectobius pallidus* overwinters as eggs in the oöthecae, the adults dying after reproducing, although it is possible that some nymphs also may overwinter. Lucas (1928) stated that *Ectobius lapponicus* (L.) overwinters as nymphs producing adults in spring or early summer. Brown (1952) found overwintering oöthecae of *Ectobius panzeri* in sand dunes in February, but no hibernating nymphs or adults. We suggest that *E. pallidus* may overwinter as nymphs because nymphs have been collected as late as November. These either die or hibernate. In addition, adults appear in early July which

seems to indicate too short a developmental period for progeny hatched from eggs in the spring of the same year. The adults are relatively short-lived. Adult females reared from nymphs collected in the field and kept with males in the laboratory lived an average of 23 days (range 6 to 61 days, N = 14); virgin females lived an average of 35 days (range 19 to 42 days, N = 14). Females lived longer than males. Very few individuals were reared to adulthood from eggs which hatched in the laboratory; we have been unable to establish a laboratory colony of this species using Purina dog chow checkers as food.

Ramme (1923) stated that it was not known whether the secretion of the tergal glands of males of species of *Ectobius* served to attract females or acted as a defensive organ to discourage enemies. In describing the mating behavior of *Ectobius,* he stated that the male runs backwards, with its elytra and wings raised vertically, toward the end of the abdomen of the female and accurately places its genitalia into those of the female. He further stated that one might assume that the male raised his wings to expose the tergal gland in order to excite the female with his glandular secretion; but Ramme believed that this was not so and that the wings were raised because in the resting position they cover the abdomen and would obstruct or even prevent union. Copulation often lasted as long as 24 hours and, according to Ramme, no spermatophore was formed. Konček (1924) stated that the tergal glands of males of *Ectobius lapponicus* and *E. sylvester* (Poda) were biologically important as a secondary sex character and mentions Sikora's (1918) observations on *Blattella germanica* as confirmation for this view.

Our observations of the mating of *Ectobius pallidus* show that Ramme's interpretation of the reproductive behavior of *Ectobius* is incorrect. The males which we observed were isolated from females for three days before being paired. When the male comes in contact with a female, he turns about, raises his wings and tegmina, extends his abdomen toward the female, brings his cerci together, and moves backwards. Even when the female has moved out of range, the male remains in a characteristic position with his head down, abdomen raised and strongly convex, and wings raised slightly away from the abdomen. If a female

passes close by, or even if touched by another male, the courting male raises and flutters his wings at about a 90° angle and pushes his abdomen backwards. A receptive female feeds on the secretion of the male tergal gland (fig. 11), and the male pushes backwards beneath the female and grasps her with his hooked phallomere. Once this is accomplished, the pair assume the characteristic opposed position (fig. 12). Contrary to Ramme's belief, a spermatophore is formed in *Ectobius*. The tergal gland of *Ectobius* functions in mating behavior just as it does in other species of cockroaches in which the males possess this structure (Roth, 1952; Roth and Willis, 1952, 1954).

In the field at Plymouth, we observed two species of ants, *Aphaenogaster picea* Emery and *Lasius alienus* (Förster) carrying off specimens of *Ectobius pallidus*.

Many of the adult cockroaches that were collected were parasitized by an undetermined species of Mermithidae. This mermithid (fig. 16) lies coiled in the body cavity of the host, and one end of the worm may extend into the thorax. The worms have been seen to leave the cockroach between the thorax and abdomen (fig. 14) or thorax and head (fig. 15). Inasmuch as the adult cockroaches are relatively short-lived, we are undecided whether the host was killed by the parasite or whether the worms left the insects after they died or became moribund from other causes. However, it is obvious that these parasites are detrimental to their hosts because some of the internal organs of the cockroaches were destroyed; the abdomens of the parasitized cockroaches from which worms emerged were essentially hollow shells. Hyman (1951) states that mermithids destroy the viscera and fat body, ". . . killing the host or rendering it incapable of metamorphosis and reproduction."

Although a large number of nematode species have been described from cockroaches, there are practically no records of mermithids parasitizing these insects. Bode (1936) stated that he found a few instances of *Periplaneta americana* being parasitized by such nematodes as "*Mermis* or *Gordius*." The only record we have found of a nematode parasitizing *E. pallidus* is *Blatticola blattae* (Graeffe, 1860) Chitwood, 1932 which is found in the intestinal tract (Chitwood, 1932).

Summary

Some field and laboratory observations on the biology of *Ectobius pallidus* are described. In Massachusetts, this cockroach apparently overwinters as eggs in the oötheca; however, possibly some nymphs may also overwinter. Adults die shortly after reproducing. The eggs apparently pass through a dormant period before absorbing water and completing development. As a result of water uptake, the oötheca increases markedly in size and changes color, becoming lighter brown, prior to the hatching of the eggs.

The mating behavior of *Ectobius pallidus* is similar to that of other species in which the males possess tergal glands; the female *Ectobius* feeds on the male's tergal gland secretion prior to copulation.

Two species of ants were found to prey on *E. pallidus*, and an undetermined mermithid parasitizes this cockroach.

Acknowledgements

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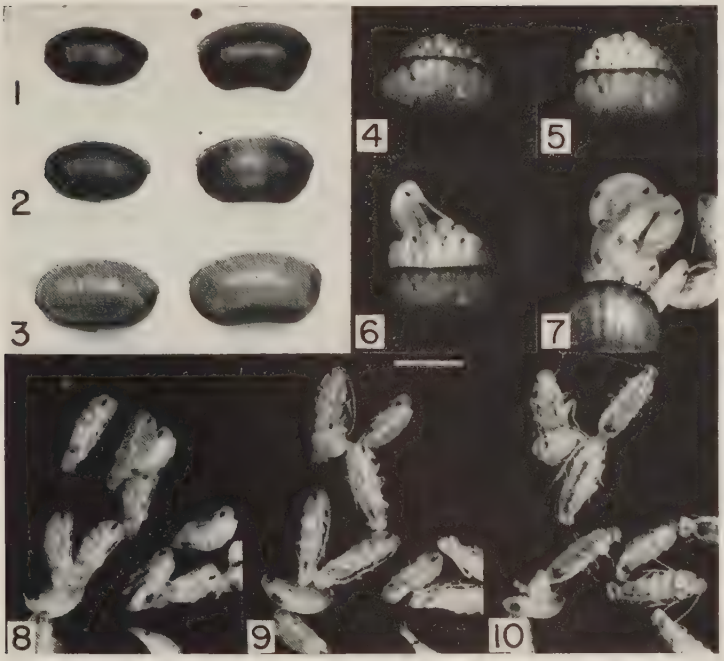

Figures 1-10. *Ectobius pallidus*. 1-3. Uptake of water through the oötheca; egg cases collected in the field 8 November 1954 and placed on moist filter paper.

1. 23 November: essentially no visible external change during the first 15 days the oöthecae were kept moist. 2. 24 November: note the increase in size of both oöthecae and the change in color down the middle of the egg case on the right where the oötheca is being stretched by the growing embryos. 3. 26 November: note the marked increase in size of the oöthecae and the complete change in color (cf. fig. 1). This was the extent to which the oöthecae swelled before the eggs hatched.

4-10. Hatching of eggs, initiated by slitting the crista of the oötheca with a scalpel. The entire sequence required 12 minutes; note in figure 8 that the pronymphs are still enveloped by their embryonic membranes which are being shed and can be seen at the tips of the abdomens of several nymphs in figure 10.

(Horizontal bar = 2 mm.)

Figures 11-13. Reproductive behavior of *Ectobius pallidus*.
11. Female (right) feeding on the secretion from the male's tergal gland. 12. Pair in copula. (Horizontal bar = 2 mm.) 13. Female carrying an oötheca; note that the oötheca was rotated so that the keel was toward the right. (Horizontal bar = 2 mm.)

Figures 14-16. Undetermined mermithid that parasitizes *Ectobius pallidus*. (Vertical bar = 5 mm.)

14. Mermithid which has emerged from between the abdomen and thorax of an adult male *Ectobius*. 15. Mermithid which has emerged from between the head and thorax of an adult female *Ectobius*. 16. Mermithid free from the host.

COMPARATIVE MORPHOLOGY OF THE ABDOMEN OF A MACHILID AND A RHAPHIDIID [1]

BY RYUICHI MATSUDA

Department of Entomology, University of Kansas, Lawrence, Kansas

Introduction

The present study deals with the external structure and the musculature of the abdomen of two morphologically important species of insects, *Neomachilis halophilis* Silvestri (Thysanura) and *Agulla adnixa* (Hagen) (Neuroptera).

The musculature of pregenital segments in the order Thysanura and Neuroptera has been poorly understood. No comprehensive study of the musculature of pregenital segments of the Thysanura has ever been undertaken, in spite of the fact that many workers studied the ventral appendages of the abdomen of this order. In Neuroptera there have been only two works treating the musculature of pregenital segments (Miller 1933, Maki 1936). Thus, our concept of the generalized musculature of pregenital abdominal segments in insects is based on insufficient knowledge of these two important orders, as was deplored by Snodgrass (1931).

As to the morphology of genital segments of pterygote insects, the genitalia of orthopteroid insects has been extensively studied by many workers. Relatively little morphological work, however, has been done on genital segments of neuropteroid insects. It was Michener (1944) who first tried to homologize the male genitalia of a neuropteran insect, *Agulla*, directly with that of Thysanura on the basis of external structures. Gustafson (1950) interpreted the genital structure of Thysanura quite differently from other workers. It seems, therefore, worthwhile to compare the genital structures of these two morphologically important species on the basis of musculature.

[1] Contribution No. 938 of the Department of Entomology, University of Kansas.

The present study was undertaken with these recent studies of the genitalia, and the present status in regard to the morphology of pregenital segments of insects in mind, in a hope of solving problems involved by working on these two primitive forms of insects.

Acknowledgements

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External Structure

Neomachilis halophilis Silvestri

Pregenital Segments (Pl. IV, A)

The first seven abdominal segments are basically the same except for the absence of the stylus in the first segment. Paired eversible sacs are on each segment. The stylus arises always lateral to the eversible sac on the posterior margin. The sternum has a tendency towards reduction in posterior segments. The intersegmental relationships are the same both dorsally and ventrally. Each segment covers the anterior part of the succeding segment and is continuous by the membranous infolding to the antecosta of the latter. The tergum, the coxite, and the sternum are distinct from each other.

Genital Segments (Pl. IV, B, C)

In the eighth and ninth segments of both sexes the eversible sacs are lacking; instead gonapophyses are present in both segments in both sexes. The stylus is present in both segments in both sexes. In the eighth segment of the male the sternum is represented by a narrow, transverse, membranous area at the base. The gonapophysis arises from near the middle of the upper margin of a membranous infolding from the posterior margin of the eighth segment. The eighth segment in the female is provided with a median basal plate which is more or less clearly de-

fined laterally; this plate is here considered as the sternum. The laterosternite is located on each anterolateral angle of the same segment. The gonapophysis arises from near the anterior end of the membranous infolding from lateral and posterior margins of the same segment. The stylus arises from the posterior margin of each coxite at the middle. The sternum of the ninth segment in the male is represented by the median basal area bordered by paired oblique carinae posteriorly, upon which the gonapophysis is connected. The phallus is basally connected with the carinae in the sternal region beneath the gonapophyses in the male. The sternum of the ninth segment in the female, in the absence of a defined median plate, is here suspected of being represented by a narrowly defined area in the middle of the basal margin. The gonapophysis arises from the point of connection of membranous infolding from posterior and lateral margins of the same segment and from the sternal region. The stylus is present on both the eighth and ninth segments. The eversible sacs are absent in these segments.

Postgenital Segments (Pl. VI, C)

The tenth segment lacks the coxosternal plate. Laterally, the tenth tergum is articulated with the ninth coxite at the anterior end of the membranous infolding on the lateral margin. The eleventh segment carries caudally the median filament and laterally the cercus. On its undersurface are soft valve-like lobes enclosing the anus; the lobes are the paraprocts which represents the sternum of the eleventh segment. A small tube, the partial remnant of the eleventh segment, arises from the base of the median filament on its ventral side.

Agulla adnixa (Hagen)

External morphology of the abdomen of this species was studied by Ferris and Pennebaker (1939).

Eleven clearly recognizable segments are seen in this species. Spiracles are present in the first eight segments.

Pregenital Segments (Pl. V, A)

The first segment is somewhat reduced ventrally, and is provided with a larger spiracle. The paratergite is clearly recog-

nized in the first and second segments as distinct sclerotized plates continuous with the dorsal sclerotized areas. There are, in the pregenital segments, dorsal and ventral sclerotized regions. Since spiracles are always located in the lateral membranous regions between the dorsal and ventral sclerotized regions, the region above a spiracle is regarded as the tergum. The ventral sclerotized region is here labelled as the coxosternum since in this species, as in many other species, the area is composite. The anterior margin of each segment, both dorsally and ventrally, is hidden beneath the posterior margin of the preceding segment. The development of the submarginal antecostal suture is weak except in the second segment where the anterior submarginal area is strongly sclerotized, and apparently the acrotergite is formed.

Genital Segments

Male (Pl. V, A; Pl. VIII C).

In the male the modification of the abdominal segments begins with the ninth. The tergum and the sternum are fused and form a complete ring. The coxite is articulated with the posterior border of the tergosternum. The gonapophysis, which is represented by the black paired plate, is connected with the basal region of each gonocoxite. The gonapophysis is not a rather short process arising from the apical region of the gonocoxite as shown by Ferris and Pennebaker (1939). The hook, which arises from the anterior margin of the gonocoxite, was called the fragmentum of the coxopodite by Ferris and Pennebaker, and later homologized by Michener (1944) with hymenopteran volsella. The phallus is rather deeply imbeded, arising from the horizontal line across the basal margin of the gonocoxite; aedeagus is tridentate; the gonopore is at the apex of the aedeagus. The stylus is borne at the apex of the gonocoxite.

Female (Pl. V, B, C).

The seventh sclerotized definitive sternum or the coxosternum is retained along the anterior margin of the same segment. The eighth segment has the ventral basal area hidden beneath the ventral posterior region of the seventh segment. The membranous region drawn out into a shaft formed by the gonapophyses

of the ninth segment was regarded as the sternite of the eighth segment by Ferris and Pennebaker (1939). This is, however, actually the almost indistinguishably fused eighth sternum and the rudimentary fused gonapophyses of the eighth segment. Ferris and Pennebaker apparently missed a rather faint but still clearly recognizable longitudinal suture on the ventral surface of each gonapophysis (in the text figure this suture is somewhat exaggerated). Also the true sternal region is recognizable by the transverse suture representing the posterior margin of the sternum. Thus, the gonapophyses of the eighth segment are directly connected with the eighth sternum in this species. This will be again discussed in connection with the musculature associated with these structures. The gonopore is open just anterior to the basal margin of the region here considered as the eighth sternum.

In the ninth segment there is a small subtriangularly defined region at the basal lateral margin of the definitive tergum. This is here considered as the valvifer. The ninth sternum is a narrow membranous region drawn out into the shaft formed by gonapophyses as they were interpreted by Ferris and Pennebaker.

Postgenital Segments (Pl. V, A)

The tenth and eleventh segments are clearly distinguishable dorsally. The sternum of the tenth segment in the female is retained as a small apodeme ventrally. The anus opens at the apex of the eleventh segment.

Musculature

Only the somatic muscles are treated in this study.

Neomachilis halophilis Silvestri

Although the musculature associated with ventral appendages of the abdomen of the order Thysanura was worked out by many workers, the musculature of the pregenital segments of this order was treated only rather fragmentarily by Grassi (1887) and Bär (1912). Maki (1938) showed the musculature of the two basal abdominal segments in his schematic drawing without explanation.

The musculature of the pregenital segments (Pl. IV, B, C; Pl. VI, A, B; Pl. VII, D).

There are three sets of muscles that occur apparently within each tergite. Two longitudinal muscles extend medially from the antecosta to that of the succeeding segment. These are internal dorsal muscles (1, 2). The external dorsal muscle (3) is represented by an oblique muscle arising near the anterior margin. This muscle is inserted near the lateral edge of the antecosta of the succeeding segment; its origin tends to split into two bundles.

Other muscles occuring in the tergal region are the bundles of muscles seen in plate VI, figure B. These muscles are unique in the sense that all component muscles of each segment are tightly and intimately attached to each other forming a sort of twisted rope throughout the entire length of the abdomen. (In the text figure the association of each muscle is rather loosely shown.) The muscles numbered 5 and 6 are located within each pregenital segment. Muscle 5 embraces muscle 6 cephalocaudally; the latter, in turn, embraces muscle 5 dorsoventrally. Muscle 7 always arises from the anterolateral region of each tergite, and extends caudoventrally for the length of two segments and attaches on the ventral region of muscles 5 and 6. This muscle (7) arising from the seventh segment inserts on the sternal region of the eighth segment in both sexes; the same muscle arising from the eighth segment apparently inserts on the sternal region of the ninth segment in the male, and on the lateral region of the ninth sternum (?) in the female. Also in the seventh segment of the female a slender muscle (8) arises in the anterolateral region of the tergum. This muscle inserts near the sternum of the eighth segment. It does not occur in the male. The muscle (4) occurs in the second through the ninth segments in both sexes, and attaches dorsally on each tergite on its median longitudinal axis behind the antecosta and between the pair of internal dorsal muscles (1). This muscle is the only one in the twisted group of muscles attaching on the integument. Muscles (5) and (6) are somewhat modified and two slender muscles are associated with them in the last three segments as will be described later. The muscle (4) is probably the homologue of Fächer Muskel of Bär (1912). Bär failed to see the ventral attachment of this muscle on the integument. The homologies of these four twisted bundles

of muscles with muscles in other groups of Apterygota, as well as Pterygota, are impossible to establish except for the muscle (7), as will be discussed later, since no such peculiar muscles have ever been described in other groups of insects. In any case, three out of four component muscles of each segment have no attachment on the integument. It is interesting to consider them from the functional point of view. In the absence of external organs or structures responsible for strong leaping action characteristic of this group of insects, this bundle of muscles which stretches throughout the entire length of the abdomen, and the attachment of the muscle (4) on each tergite, strongly lead one to the supposition that this unique set-up of the abdominal musculature is directly responsible for characteristic strong leaping action.

Lateral muscles (Pl. VI, A).

In this species the lateral muscles are apparently the tergocoxal muscles. In each segment from the first to the seventh there are present two bundles of muscle fibers arising from the lateral region of each tergite and inserting ventrally on the coxite near or beneath the muscles of the stylus and the eversible sac (8, 9). These muscles are confluent ventrally in the fifth to seventh segments.

Ventral muscles (Pl. VII, D).

The muscle of the stylus (14) and that of the eversible sac (15) arise from the anterior region of the coxite. In the absence of the stylus in the first segment, the muscle of this structure is lacking.

The Musculature of the Genital Segments
(Pl. IV, B, C Pl. VI, C, D)

Dorsal muscles.

The internal dorsal muscles are as in the pregenital segments; they extend between antecostae. However, the presence of a short muscle in the ninth segment (10) should be noted. This muscle originates in anterior region of the ninth tergite above one of the internal dorsal muscles (2), and inserts on the antecosta of the same segment. The external dorsal muscles are represented by two distinct muscles which are inserted in the lateral

region of the antecosta at the same place as in pregenital segments. The external dorsal muscle in the tenth segment inserts on the antecosta of the eleventh segment, not directly on the cercus as in some pterygote insects. The muscle (5) in the genital segments extends between the anterior region of the ninth segment and the eighth segment. This muscle embraces cephalocaudally the anterior region of the twisted bundle of muscle fibers which attaches posteriorly on the ventral posterior margin of the tenth segment (11). One slender muscle (12) extends between the posterior region of the ninth tergite and a point beneath muscle (5) of the eighth segment. Another slender muscle (13) extends between the area beneath muscle (5) and the ventral posterior margin near middle of the tenth segment.

The lateral and ventral muscles are different in the male and female, and are described separately.

Male (Pl. IV, C).

In the eighth segment the gonapophysis receives a slender muscle from the gonocoxite. The muscle of the stylus is the same as in pregenital segments. In the ninth segment the gonocoxite receives five muscles from the ninth tergite. The anterior lateral muscle (8) in this segment is represented by two distinct bundles of muscle fibers. The posterior bundle is inserted on the anterolateral angle of the ninth gonocoxite; the anterior one is inserted on the sternal region. The posterior lateral muscle (9) goes deep into the gonocoxite and inserts on the membrane near the lateral margin of the phallus. The anterolateral angle of the ninth gonocoxite also receives a slender muscle (16) coming from the posterolateral region of the ninth tergite. Another muscle (17) coming from the anterolateral region of the ninth tergite inserts on the point of articulation between the ninth and tenth segments. There also arises a slender muscle (18) going near the base of the gonapophysis from the ventral point of articulation between the ninth and tenth segments. Two small muscles (19, 20), arising from the anterolateral angle of the gonocoxite, attach near the lateral margin of the phallus. The muscle of the gonapophysis (21) arises from near the oblique carinae delimiting the sternal region posteriorly.

Female (Pl. IV, B).

In the eighth abdominal segment the gonapophysis has a muscle originating from the base of the sternite (21). The sternal region of the eighth segment also receives a slender muscle originating in the seventh tergite (8). A broad muscle originating from anterolateral angle of the laterosternite (23) inserts on the sternal region (?) of the ninth ventral plate inside the point of attachment of the muscle coming from the eighth tergite (7). In the ninth segment the gonapophysis is musculated from the base of the sternite. The differences of the female musculature from that of the male are: absence of the small muscles (19, 20) going near base of the phallus from the anterolateral angle of the gonocoxite, absence of a small muscle (16) from the posterolateral region of the tergite to the anterolateral angle of the gonocoxite, and absence of a muscle (18) from the point of articulation between the ninth and tenth tergites to near base of the gonapophysis.

Muscles of the Eleventh Segment (Pl. VI, D)

Two muscles occur in the coxal region of the eleventh segment; one of them (24) arises from the antecosta, goes horizontally caudad over the muscle (25) which attaches on the basal half of the tergum. One of the anterior bundle of fibers (27′) inserts on the basal lateral margin of the median filament; another bundle of muscle fibers arising from beneath the muscle (26) inserts on the partial remnant of the twelfth segment. The cercus has no muscle directly from either eleventh or tenth segment. The tergal muscle or muscles attached on the antecosta of the eleventh segment must activate the cercus.

Agulla adnixa (Hagen)

Pregenital Segments

The musculature of pregenital segments of neuropteran insects was worked out by Miller (1933) for *Chrysopa,* and by Maki (1936) for *Chauliodes.* The modification of the abdominal musculature begins with the eighth segment in the female and the ninth segment in the male. As the first segment also shows a considerable difference from the succeeding segments, the musculature of this segment is described separately.

The First Segment (Pl. VII, C, Pl. VIII, A)

Dorsal muscles.

There are six pairs of muscles which occur within the tergal region in addition to the one for the spiracle. A slender muscle (28) is attached to the homologous muscle in the next segment. Two thick muscles (29, 30) connect the metathoracic postnotum and the antecosta of the second segment. Another thick muscle (31) arises distinctly from behind the anterior margin of the first segment. The muscles that occur lateral to the preceding muscles (32, 33) are apparently intersegmental. A fine muscle (34) extending from the anterolateral region of the tergite inserts on the apical part of the sclerotized paratergite. In the lateral region of the first segment there occur four slender muscles (35, 36, 37, 38) which insert on anterior margin of the paratergite of the second segment. These muscles are probably homologous with a thin longitudinal bundle of muscle fibers covering the lateral membranous wall in succeeding pregenital segments (46). In the coxosternal region occur two thick intersegmental ventral muscles (39, 40) and one small oblique muscle (41) inserting on the upper anterior angle of the coxosternum of the second segment. The occulsor muscle of the spiracle (42) arises from the first tergite and the dilator of the spiracle (43) arises from the sternal apophysis of the metathorax.

Second to Eighth Segments (Pl. VII, C Pl. VIII, A, B)

The description of the typical abdominal musculature is somewhat difficult due to the presence of a huge dorsal muscle stretching for three segments behind the first segment, and to the gradual reduction in number of muscles in the posterior segments.

The fine internal dorsal muscle (28) also occurs in the second, third, and fourth segments. This muscle is attached posteriorly to the same muscle in the succeeding segment. A huge internal dorsal muscle (44) stretches from the well-carinated antecosta of the second segment to the anterior region of the fifth segment. This muscle is probably homologous with the muscle (29) in the first segment. One of the dorsal muscles (30) is lost from the sixth segment on. Another dorsal muscle (31) persists throughout all segments; the origin of this muscle is behind the anterior

margin of the segment from the third segment on. The innermost dorsal longitudinal muscle (29) is always intersegmental and persists throughout all abdominal segments. The lateral dorsal muscles (32, 33) always arise from the lateral margin of the sclerotized tergites; their points of posterior attachment gradually shift ventrally in posterior segments. Although points of attachment of these muscles in posterior segments may be coxal in origin, they are apparently homologous with the muscles labelled as (32), (33) in anterior segments in which they are apparently within the tergal region. A muscle of doubtful homology labelled (41) occurs in the eighth segment of the male. There always occurs a short muscle or a few bundles of muscles (45) in the lateral membranous region in the third to eighth segments; these muscles insert on the antecosta of the succeeding segment lateral to the external dorsal muscles (31).

Lateral Muscles (Pl. VIII, A, B)

The lateral membranous region in the second to seventh segment (female) or to the eighth segment (male) is totally provided with a thin longitudinal sheet of muscle fibers (46) as is shown in the fifth segment in text figure. There is no special muscle for the spiracle from the second segment on. This sheet of muscle fibers as a whole is probably responsible for occulsion and dilation of the spiracle. There also occurs an oblique muscle (42) [2] connecting the lateral margins of the sclerotized tergal region and the sclerotized ventral coxosternal region in the second to fifth segments.

Ventral Muscles (Pl. VIII, A, B)

Ventral longitudinal muscles (39, 40, 47) are represented by three bundles of muscle fibers in the second and third segments and by two bundles in the succeeding segments. These muscles arise from behind the anterior margins of the third to seventh segments. These muscles, in the female seventh segment, are apparently attached on the ventral region of the coxosternum and the anterolateral angle of the sternum in the eighth segment.

[2] On plate VIII A are three muscles numbered 44, across the center of the figure transversely. These should be numbered 42 (those referred to here).

The Musculature of Genital Segments

Male (Pl. VIII, C, D). As noted in the description of the external structure, the gonocoxite of the ninth segment in this species is clearly separated from the fused anterior tergosternal ring. This makes the analysis of origins and insertions of muscles in terms of sclerites simpler than in other groups of the order Neuroptera.

Muscles Inserted on the Gonapophysis.—A thin muscle arising from the middle of the sternal region (48) inserts on the base of the gonapophysis. A huge bundle of muscle fibers (49) arising from the ventral surface of the gonocoxite inserts on the basal region of the gonapophysis. Another thin muscle (50) arising from the cavity of the fragmentum of the gonocoxite inserts along the membrane on the posterior lateral margin of the gonapophysis.

Muscles Inserted on the Gonocoxite.—One thin muscle arising from the sternum (51) inserts on inner basal margin of the gonocoxite and probably on a part of the base of the gonapophysis.

Muscles Inserted on the Fragmentum of the Gonocoxite.—One thick fan-shaped muscle (52) originating from the lower part of the tergosternum inserts on lateral edge of the fragmentum of the gonocoxite. This muscle is probably the sternocoxal.

Muscles Inserted on the Stylus.—One fan-shaped muscle (53) originating from the upper basal area of the gonocoxite above the transverse suture inserts on the upper angle of the stylus. Another muscle (54), originating from the gonocoxite beneath the transverse suture, inserts on the lower basal cavity of the stylus.

Muscles Inserted on the Phallus.—One muscle (55) originating from the basal region of the gonocoxite goes beneath the lower muscle of the stylus (54) to insert on the base of the phallus. Another muscle (56), originating from the lower portion of the tergosternum, stretches posteriorly into the inner lateral wall of the phallus.

Other Muscles.—One thick short bundle of muscle fibers (57) arises from the upper portion of the ergosternum and inserts on the upper basal margin of the gonocoxite and the ventral region of the tenth segment. In the upper dorsal region occurs a dorsal

muscle (58) which inserts on the antecosta of the tenth segment. Another slender muscle (59), arising from the basal tergal region, extends posteriorly as far as the apical region of the eleventh segment above the anus. The longitudinal dorsal muscle (61), arising from the basal region of the tenth segment, extends as far as the apex of the eleventh segment. Another dorsoventral muscle (60) occurring in the eleventh segment is attached on the anus.

Female (Pl. VII, A, B). In the female, specialization begins with the eighth segment. The dorsal musculature is essentially the same as in the preceding segment. Two muscles (63, 64), arising from the posterior region of the ninth segment, insert on the point of articulation between the basal lateral angle of the sternum and the gonocoxite. A small muscle (62), arising from the coxosternal region of the seventh segment, also inserts on the same point. Two muscles (65, 66) arising from behind the posterior margin of the eighth definitive tergite just beneath the spiracle, insert on the anterior margin of the valvifer. A pair of thin muscles (67), originating from the base of the sternum, insert on the rudimentary gonapophyses. In the ninth segment two dorsal muscles insert on the antecosta of the ninth tergite. Two small longitudinal muscles (68, 69), arising from the basal region of the ninth tergite, insert on the valvifer. Another small muscle (70), arising from the ninth definitive tergite posterior to the two preceding muscles, inserts on the upper basal margin of the gonapophysis. A slender muscle (71), arising from the posterior margin of the valvifer, goes horizontally caudad to insert on the ninth sternum beneath the point of dorsal union of the second gonapophysis. Another two muscles, one thick (73) and one slender (72), are inserted on the apodeme of the ventral region of the tenth segment. All muscles occurring in the tenth and eleventh segments in the male (59, 60, 61) also occur in the female.

Discussion

Pregenital Segments

Homologies of dorsal muscles in *Neomachilis halophilis* Silvestri with those in pterygote insects can be rather easily estab-

lished. The occurrence of a huge internal medial dorsal muscle which stretches for three segments in *Agulla adnixa* (Hagen) must be the fusion product of three muscles which has resulted from extremely weak development of the antecosta in this species. This muscle, therefore, can be regarded as primitive rather than specialized. Miller (1933) describes in *Chrysopa prolabunda* the same muscle which extends through the length of the first segment as far as the middle of the second segment. Dürken (1907) shows, in *Ephemerida ignota,* a dorsal muscle which takes its origin on the middle of the tergum and crosses the following segment to be inserted on the anterior margin of the second tergum. Dürken calls this a compound intersegmental muscle. The occurrence of this compound muscle in one other primitive order, Ephemerida, strengthens the view here maintained. No occurrence of such compound muscle was reported by Maki (1936) in *Chauliodes formosanus.*

The occurrenc of a twisted bundle of muscles which stretches throughout the entire length of the abdomen in *Neomachilis halophilis* Silvestri has apparently escaped the effect of abdominal segmentation. This is seen from the fact that three out of four component muscles have lost the attachment on the integument, and one of the component muscles (7) extends for the length of two segments posteriorly in the first six segments. Since in this species the antecosta is well developed in each tergite, the attachment of muscles to each other and the extension of one of the component muscles for two segments, they are apparently of a different nature from the composite muscle in *Agulla adnixa* (Hagen). This set of muscles in *Neomachilis halophilis* Silvestri can, therefore, be regarded as an adaptive specialization for the characteristic leaping action in this species.

The occurrence of an external sheet of thin longitudinal muscle fibers covering the entire lateral wall in *Agulla adnixa* (Hagen) is apparently unique to this species. Occurrence of no such muscle is known in adult insects as far as the writer is aware. This apparently undifferentiated sheet of muscle fibers reminds one of the intricate musculature of some groups of immature insects.

The lateral muscles in *Neomachilis halophilis* Silvestri (8, 9) are apparently morphologically the tergocoxal. Distinct differ-

entiation into the tergum, the coxite and the sternum in this species makes the analysis of morphological arrangement of these muscles quite simple. These muscles are probably homologous with the muscle (42) [3] in *Agulla adnixa* (Hagen).

The ventral muscles are always inserted on the eversible sacs and on the styli in *Neomachilis halophilis* Silvestri. It should be remembered in this connection that Gustafson (1950) homologized the eversible sac and its associated muscle to the gonapophysis and its associated muscle. If these homologies are correct, one of the ventral muscles in the pregenital segments of *Agulla adnixa* (Hagen), probably the internal medial, can be homologized with the muscle of the eversible sac in Thysanura because the homologous muscles in the eighth segment in the female of both species insert on the same structure, the gonapophysis. This homology, however, does not seem to be tenable. In spite of Gustafson's statement (p. 40) "the origin of the musculature of the eversible sac is usually on the sternum or the laterosternite," the muscle attachment of these structures in *Neomachilis halophilis* Silvestri does not substantiate this view; the muscle of the gonapophysis arises from the anterior region of the coxite although it is approximated to the sternum. In all morphological works treating the genital segments of the Thysanura, including Gustafson's text-figure, the muscle of the eversible sac is always confined to the coxite. The eversible sac cannot be homologous to the gonapophysis as far as the musculature indicates.

Genital Segments

The order Thysanura has been always considered as possessing the basic structures in genital segments from which the genital segments from which the genital structures of pterygote insects have been derived. Direct homology of the thysanuran genital segments with those of the male of *Agulla* was first attempted by Michener (1944). Later, Gustafson (1950) also pointed out the primitiveness of male genital segments in the genus *Agulla*.

[3] See footnote 2.

Female

In *Neomachilis halophilis* Silvestri both the anterior and posterior gonapophyses arising from eighth and ninth segments are distinctly articulated with the sternal region and are musculated from the basal part of the sternum. Turning now to *Agulla adnixa* (Hagen) it will be immediately noticed that the same situation exists in the eighth segment. The rudimentary gonapophyses are musculated from the base of the eighth sternum. Occurrence of the same condition was recently reported by Byers (1954) in *Bittacus*. It should be also noted that Snodgrass (1903) suspected that the prolonged process arising from the eighth sternum was the rudimentary gonapophyses in Tipulidae (Diptera); Rees and Ferris (1939) clearly designated this structure as the gonapophysis of the eighth segment in *Limonia sciophila* (Tipulidae, Diptera).

Thus, the direct homology of the gonapophysis of the Machilidae of Thysanura and that in lower groups of three orders of Neuropteroid insects, both in external structure and musculature in the eighth segment of the female, has been here established. In some orthopteroid insects and in Hymenoptera, while retaining the gonapophysis in both the eighth and ninth segments in many groups, the structure associated with the basal part of the gonapophysis in the eighth segment has apparently undergone a great modification.

In the ninth segment of *Agulla adnixa* (Hagen) the connection of the gonapophysis is with a small subtriangular part continuous with the definitive tergum which is here considered as the homologue of the valvifer in other orders. This part is interpreted as a part of the true sternum in this work and so labelled.

Two alternatives are possible for the morphological assignment of this part, either sternal or coxal. Practically all morphologists accept the latter view on the theoretical ground that the valvifer is the structure which bears the coxal limb, therefore, this structure is morphologically the coxite. No morphologist, as far as the writer is aware, has ever consciously attempted to interpret morphologically the valvifer in terms of the former alternative. The female genital segments of *Agulla adnixa* (Hagen), in which the sternum is clearly separated and

without valvifers in the eighth segment, afford ideal material for the test of the validity of these two alternatives.

Let us try first to homologize the associated musculature of the valvifer with the associated musculature of the sternum and gonapophysis of the eighth segment following the first alternative. If the area in question is a part of the sternum, the muscle (71) arising from the posterior margin of this area and inserting on the ninth sternum at the point of dorsal fusion of gonapophyses can safely be regarded as homologous with the muscle (67) between the basal margin of the eighth sternum and the base of the gonapophyses; the muscles (65, 66) which extend from the definitive eighth tergum to the basal margin of this triangularly defined valvifer in the ninth segment can also be regarded as the homologue of the small muscle (62) arising from the definitive seventh tergum (or coxosternal region) and inserting on the point of articulation between the definitive eighth tergum and the sternum. Homologies between muscles (63, 64) in the eighth segment and muscles (68, 69) in the ninth segment also become possible since both of these groups of muscles are inserted at basal lateral angles of the sternum or the valvifer from the definitive tergum.

If, however, we follow the latter interpretation which regards this part as coxal in origin, then the muscle (71) in the ninth segment is coxal, while its equivalent muscle in the eighth segment (67) is undoubtedly sternal; the muscles (65, 66) are tergocoxal and the equivalent muscle (62) arising from the seventh segment is tergosternal, etc. Thus, homologies of these muscles become immediately impossible.

It should also be remembered that the muscle (7), which arises from the lateral region of the seventh and eighth tergites in *Neomachilis halophilis* Silvestri, is inserted on the sternal region of the next segment. This is true also in *Agulla adnixa* (Hagen) as will be seen from the morphological arrangement of muscles (62, 65, 66) in the discussion above. In the absence of attachment of the muscle (7) on the integument in *Neomachilis halophilis* Silvestri, we can not determine the point of origin of this muscle in terms of sclerites, but judging from the location of the origin of this muscle it probably arises primitively from lateral

portion of the tergum or from lateral portion of the coxite. This condition is also true of the muscles (62, 65, 66) in *Agulla adnixa* (Hagen) with which we are here concerned. Muscles (65, 66) can either be coxal or tergal in origin because they arise from just beneath the eighth spiracle, although the equivalent muscle (62) in the seventh segment is more likely the coxal muscle. Despite a slight difficulty in determining origins of the muscles here questioned, they are very probably homologous muscles. What happened to these muscles in orthopteroid insects remains to be investigated; the writer failed to recognize the homologous muscles in Ford's work (1923). Homologies of most muscles associated with the sternum and the gonapophysis in genital segments of these two primitive forms of insects now seems to have been established and it is strongly indicated that the valvifer is a part of the sternum.

Suspecting that the small triangular area in the ventral region of the ninth segment of *Agulla adnixa* (Hagen) was an incipient stage in the evolution of the valvifer, reference was made to pertinent literature to confirm the indication obtained in this study. It was immediately found that the history of opinions concerning the morphology of the insect ovipositor would occupy more space than is justifiable. A good review was given by Snodgrass (1931), and by Gustafson (1950), so that more detailed information can be obtained from these sources. The only important literature which is deemed pertinent to the following discussion is cited below.

First, attention should be called to the discovery by Heymons (1896a, b, 1899); he showed and stressed that the gonapophysis is of quite independent origin from the segmental limb, and arises from the primary sternum.

Morphologists have noticed that the gonapophysis and the valvifer arise from eighth and ninth sterna. For instance, Walker (1919) concludes that the ventral valves arise from the posterior margin of the eighth sternum as seen in *Ceuthophilus* and the valves from the ninth segment, also from the ninth sternum. He also says, in the same paper, that the valvifer represents the lateral part of the ninth sternum on the basis of observation of postembryonic development of the ovipositor. These structures,

however, *theoretically* a part of the coxite as is evidenced from his statement (1922, p. 59) "Ninth sternum represented mainly by the two elongate styligerous coxites, the lateral gonapophyses, and median pair of appendages, the posterior gonapophyses." Ford (1923) and Walker (1943) also conclude, on the basis of the studies of musculature and external structures, that the valvifer is ninth sternal in origin without referring to the basic concepts involved. Snodgrass (1935, Grasshopper abdomen, pp. 49-51), while observing the ovipositor arising from the sternal region of eighth and ninth sterna in the postembryonic development of the Gryllidae, tries to make the facts fit with the theoretical origin of the ovipositor from the segmental limb, concluding that the first valves are gonapophyses of the first gonopod, etc. Essentially the same sort of interpretation rooted upon preconception of the origin of the ovipositor from the segmental limb is seen in most, practically all, works treating the postembryonic development of genital structures in insects, of which Qadri's extensive work on Orthopteroid insects (1940) is a conspicuous example.

It will be noticed from the above review concerning the origin of the ovipositor and the associated structure that all these authors came to more or less the same conclusions in regard to the origin of gonapophysis and valvifer as that reached in the present work before they tried, *secondarily*, to interpret the facts obtained in their studies in terms of the theoretical origin of the ovipositor from the segmental limb. The present study of the muscles associated with the eighth and ninth sterna, valvifer, and gonapophysis clearly indicates that homologies of the muscles are possible only when we discard the concept of the limb origin of the gonapophysis and valvifer.

It should be pointed out again and again that the primary source of confusion in regard to the homology of the ovipositor in insects is the adherence to the concept of origin of the ovipositor from the segmental limb. If we discard this concept and replace it by the concept of independent origin of the gonapophysis from the segmental limb, as was originally proposed by Heymons (1896a, b, 1899), homologies of structures in genital segments derived from the comparative morphology of adult in-

sects will become increasingly concordant with those derived from the study of postembryonic development of the structures here concerned.

It is here maintained that the valvifer in the ninth segment of *Agulla adnixa* (Hagen) is a part of the true sternum. The valvifer in other groups of insects, though highly developed, seems to be homologous with the valvifer in the ninth segment in *Agulla adnixa* (Hagen). The muscles arising from the tergum of the same segment also always insert on the valvifer in other orders. What happened to the muscles from the tergum of the preceding segment to the sternum or the valvifer of the next segment seen in *Neomachilis halophilis* Silvestri and *Agulla adnixa* (Hagen) in other orders remains to be investigated in terms of the concept here accepted. The term valvifer apparently needs a refinement. The concept of the valvifer here maintained is restricted to the structure at base of the gonapophysis and it is ontogenetically sternal in origin in the eighth and ninth abdominal segments.

In conclusion, the indication obtained from the present study is that the valvifer is the secondary development from the sternum which has reached its highest degree of complexity in some orthopteroid insects and Hymenoptera. The gonapophysis, of which the ovipositor is composed, is connected with the true sternum in all orders of insects. More detailed discussion in regard to the origin of the insect ovipositor will be attempted in the near future.

Male

In *Neomachilis halophilis* Silvestri, in the ninth segment the gonapophysis is connected with the oblique carina bordering posteriorly the region considered to be the true sternum and receives a muscle (21) from this carina. In *Agulla adnixa* (Hagen) the basal part of the gonapophysis arises from the basal margin of the gonocoxite immediately behind the membranous region which can be, with all probability, regarded as the sternum, and has a muscle from the middle of the basal margin of the ventral surface of the sclerotized ninth tergosternum. Although the sternum and the tergum are completely fused, forming a basal ring

of the ninth segment, the point of origin of the muscle (48) inserting on the base of the gonapophysis is also, by all criteria, in the genuine sternal region.

As seen from the above the very similar point of connection of the gonapophysis and the same musculature inserted on the base of the gonapophysis convinces us that the gonapophyses in the male of both species are homologous structures.

It should be noted, however, that the gonapophyses in the females of both species have a muscle from the base of the sternum, and in the male the muscle comes from a rather posterior region of the eighth sternum, and also the connection of the gonapophyses with the sternum is more clearly recognizable in the female. This does not, however, hinder the homology of these parts in both sexes as will be discussed below.

Since there occurs no such structure as the valvifer in the female of *Neomachilis halophilis* Silvestri, and in all males of insects, the view of the sternal origin of the valvifer maintained in this study is rendered slightly difficult to substantiate by comparing the structure and the associated musculature between the both sexes and species. But as will be noted in plate IV, figure C, the muscle of the gonapophysis (21) in the male of *Neomachilis halophilis* Silvestri arises from the posterolateral margin of the sternum. This is very true in the ninth segment of the female of *Agulla adnixa* (Hagen), in which the muscle of the gonapophysis (71) (Pl. VII, B) arises from the lateral area of the sternum, if the valvifer represents the lateral portion of the sternum. Between the ninth segments in the male and female of *Agulla adnixa* (Hagen) the homology of the muscles is a little harder to establish, but still seems to be possible. The muscle (48) (Pl. VIII, C) of the male very probably arises from the true sternum, in spite of fusion of the tergum and sternum as noted previously, and is inserted on the gonapophysis; this is true in the ninth segment of the female (71) (Pl. VII, B) of *Agulla adnixa* (Hagen) if the structure here considered as the valvifer is a lateral part of the sternum.

The fact still remains, however, that the gonapophyses of the ninth segment of the male in both *Neomachilis halophilis* Silvestri and *Agulla adnixa* (Hagen) are connected with the region

which can be interpreted either as the posterior limit of the true sternum or the anterior limit of the gonocoxite, and this condition may favor the idea that the gonapophysis is primitively the structure of the gonocoxite, but the associated musculature in both sexes in both species seems clearly to indicate that they are sternal structure as discussed above. The obscurity of homology of the gonapophysis between the sexes is directly attributable to the absence or nondifferentiation of the valvifer in the male. The apparent connection of the gonapophysis with the gonocoxite must be of superficial nature as Gustafson (1950) claims.

In both species the stylus receives a muscle from the basal region of the gonocoxite (14, 53, 54).

Dupuis (1950) classified various types of ontogenetic development of male genital structures in male insects, and tried to derive the male genitalia from the tenth abdominal limb. This problem will be discussed in a separate paper.

Summary

Important results gained from the present study are as follows:

1. The external structures and musculature of the abdomen of *Neomachilis halophilis* Silvestri and *Agulla adnixa* (Hagen) were compared and homologies were attempted.
2. In the female of *Agulla adnixa* (Hagen) the presence of the eighth true sternum and the rudimentary gonapophyses of the same segment was established.
3. The connection of the gonapophysis in the eighth and ninth segments in the female of *Neomachilis halophilis* Silvestri and the connection of the gonapophysis in the eighth segment in *Agulla adnixa* (Hagen) are with the true sternum and the gonapophyses were found to be musculated from the base of the eighth sternum. Reference to literature has revealed that the same condition exists in Mecoptera and lower groups of Diptera.
4. It was found that homologies of the muscles associated with the gonapophyses and valvifer in the ninth segment and the muscles of gonapophyses and sternum of the eighth segment in *Agulla adnixa* (Hagen) become possible only when we discard the concept of the origin of the gonapophysis from the

coxite and replace it by a concept of independent origin of the gonapophysis and of the segmental limb.

5. It was concluded that the valvifer is a secondary development from the sternum, and the gonapophyses are connected with the true sternum in all orders of insects.
6. The gonapophyses in the ninth segment of the male of both species were found to be musculated from the sternum, and the comparison of the muscles attached on the gonapophyses in both sexes and species also indicates that the valvifer in the female is sternal in origin.
7. It was indicated that the eversible sac in Thysanura can not possibly be homologized with the gonapophysis, as Gustafson contends, as far as the musculature indicates.
8. The occurrence of a medial dorsal muscle which extends for three basal segments after the first segment in *Agulla adnixa* (Hagen) was noted.
9. The occurrence of a twisted bundle of muscles which stretches throughout the entire length of the abdomen in *Neomachilis halophilis* Silvestri was noted. This twisted bundle of muscles is considered as being directly responsible for strong leaping action in this group of insects.

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Explanation of Figures

Plate IV

A. Ventral view of the abdomen of *Neomachilis halophilis* Silvestri (external structure).
B. Ventral view of the female genital segments of *Neomachilis halophilis* Silvestri (musculature).
C. Ventral view of the male genital segment of *Neomachilis halophilis* Silvestri (musculature).

Plate V

A. Lateral view of the male abdomen of *Agulla adnixa* (Hagen) (external structure).
B. Ventral view of the female genital segments of *Agulla adnixa* (Hagen) (external structure).
C. Lateral view of the female genital segments of *Agulla adnixa* (Hagen) (external structure).

Plate VI

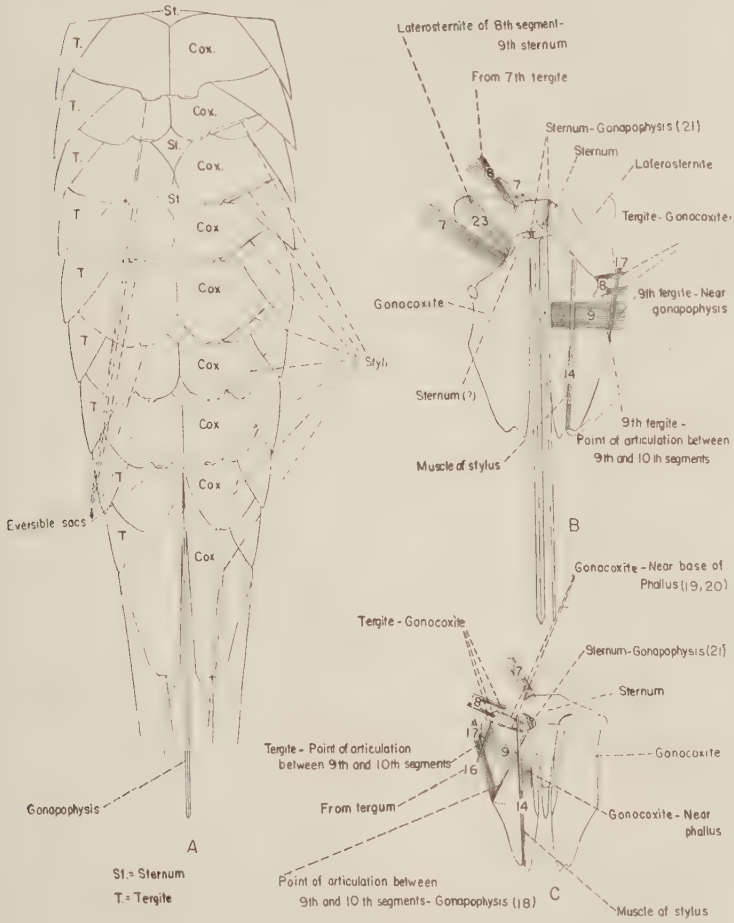
A, B. Lateral view of the pregenital segments of *Neomachilis halophilis* Silvestri (musculature).
C, D. Lateral view of the genital segments of *Neomachilis halophilis* Silvestri (musculature).

Plate VII

A. Lateral view of the female genital and postgenital segments of *Agulla adnixa* (Hagen) (musculature).
B. Ventral view of the female genital segments of *Agulla adnixa* (Hagen) (musculature).
C. Dorsal view of the pregenital segments of *Agulla adnixa* (Hagen) (musculature).
D. Ventral view of the male pregenital segments of *Neomachilis halophilis* Silvestri (musculature).

Plate VIII

A. Lateral view of the first to fourth abdominal segments of *Agulla adnixa* (Hagen) (musculature).
B. Lateral view of the male fifth to eighth abdominal segments of *Agulla adnixa* (Hagen) (musculature).
C. Ventral view of the male genital segment of *Agulla adnixa* (Hagen) (musculature).
D. Lateral view of the male genital and postgenital segments of *Agulla adnixa* (Hagen) (musculature).



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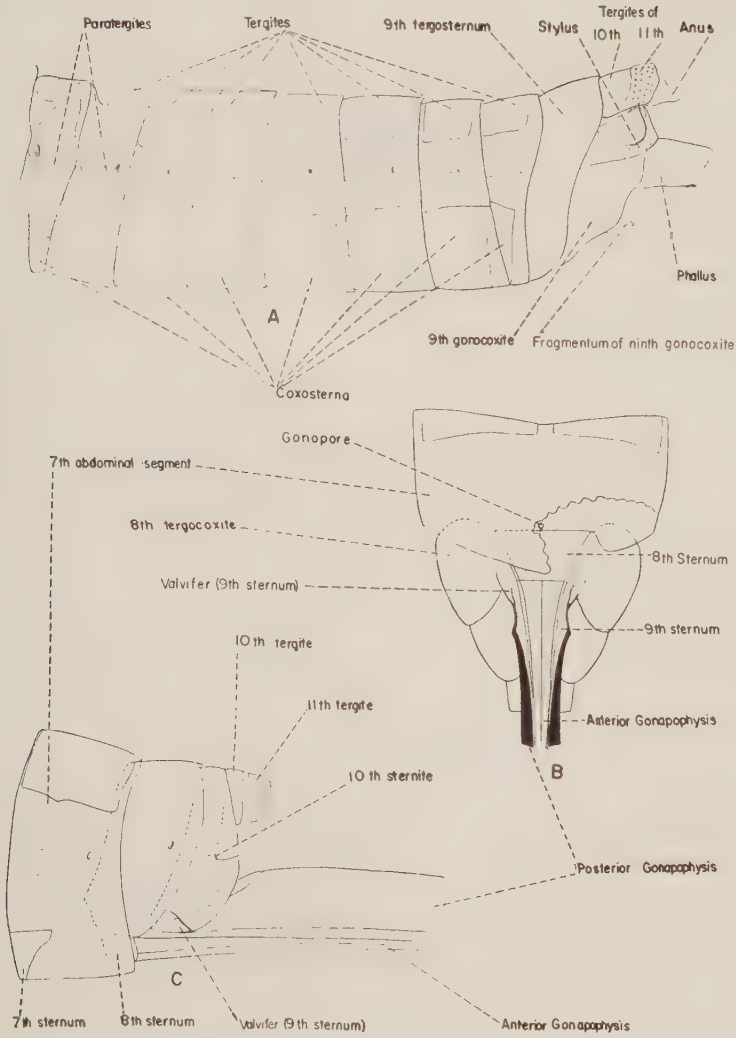

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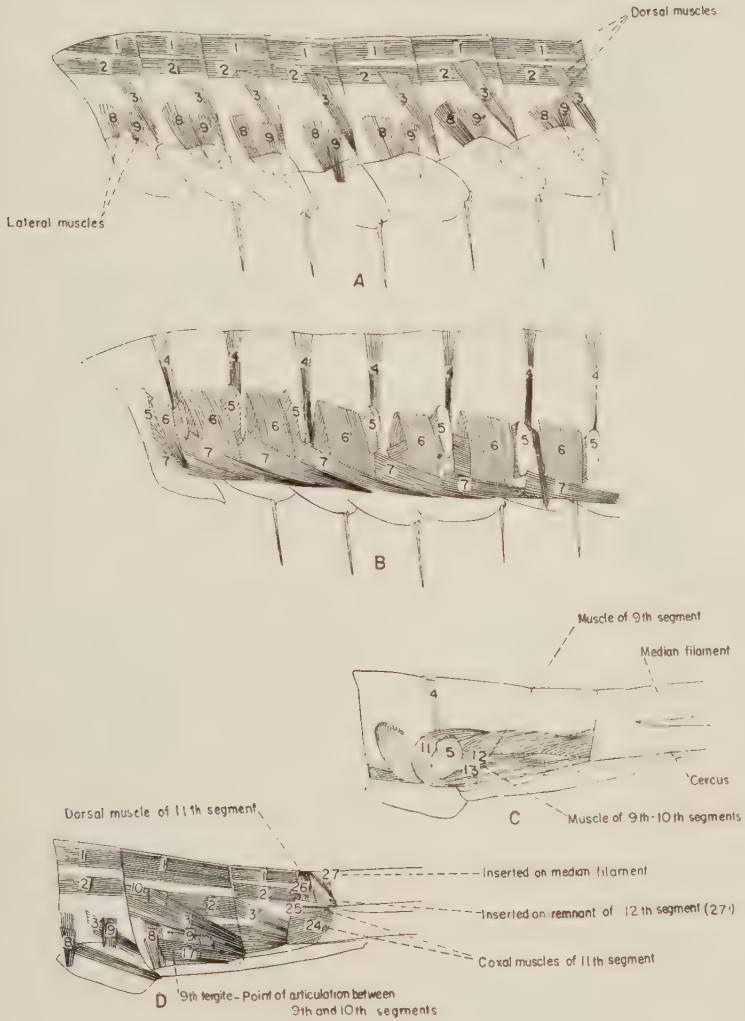

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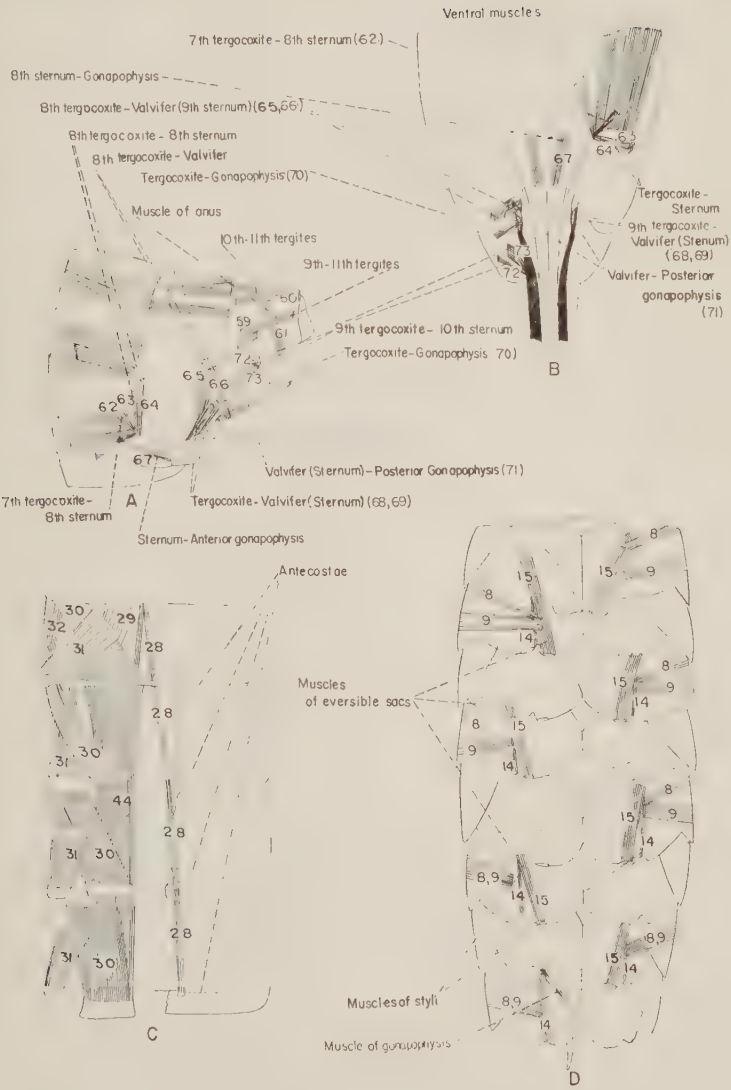

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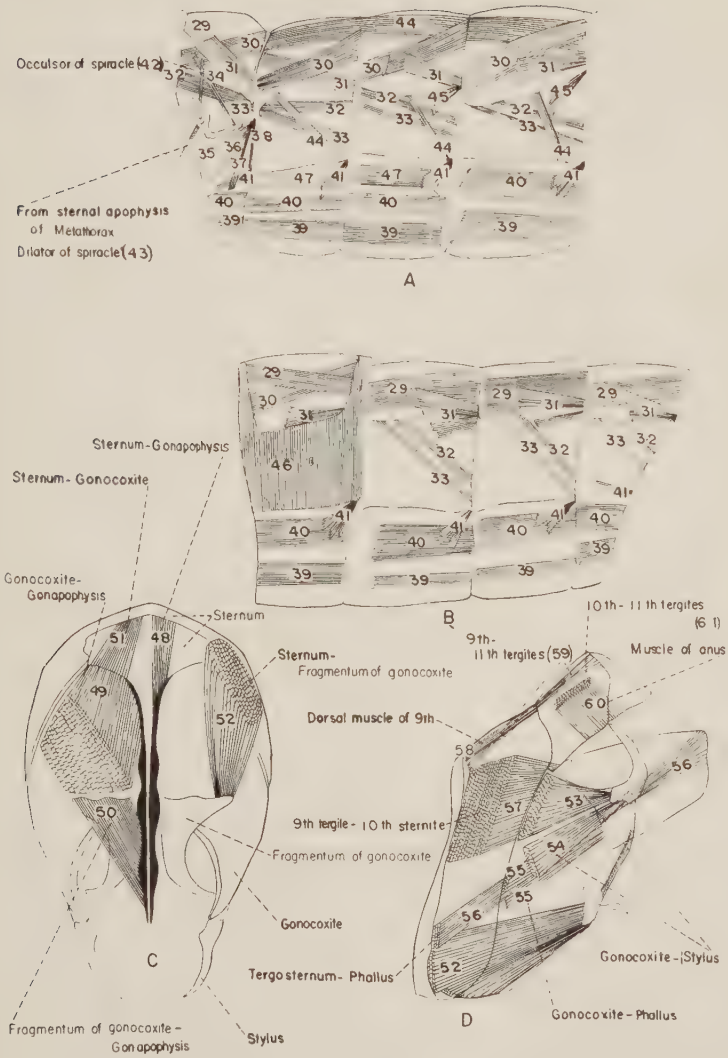

MATSUDA: MORPHOLOGY OF ABDOMEN

THE TAXA OF CAMPSOMERIS (HYMENOPTERA: SCOLIIDAE) OCCURRING IN THE NEW WORLD

BY J. CHESTER BRADLEY

Key to Subgenera

1a. Hind tibial spurs in each sex very unequal in length, acute or spatulate but not cuneiform ..... (2)

b. Hind tibial spurs of each sex short, of almost equal length, cuneiform, black ..... *Sphenocampsomeris,* subg. nov.

2a. Areae laterales of the propodeum not striate ..... (3)

b. Areae laterales of the propodeum coarsely, obliquely channeled; apical spurs of hind tibiae black ..... *Rhabdotomeris,* subg. nov.

3a. Scapulae immaculate, or in the males often with a stripe; rarely each with a large triangular or yellow spot, but in that case terga 1, 2, and 3 have each a pair of large spots and the wings have a strong fuscous pre-apical spot; the front of the male not, or but feebly, divided ..... (4)

b. Scapulae each with a pair of round dots, wanting in rare individuals; at least terga 1-3 of the ♀, 1-5 of the ♂, banded with yellow or orange-yellow; the wings without a pre-apical fuscous spot. Front of the ♂ deeply divided by a median groove, on each side of which there is an impunctate polished tubercle

Subg. *Campsomeriella* Betrem; group of *C. pilipes*

4a. Males ..... (17)

b. Females ..... (5)

5a. Posterior tibial spurs black ..... (8)

b. Posterior tibial spurs white or reddish testaceous and translucent (6)

6a. At least the tibiae and tarsi red and the apical sternal vestiture coppery; wings with a preapical cloud, which occasionally is feeble (7)

b. Legs entirely black; all sternal vestiture white or black; wings without a preapical cloud; longer hind tibial spur feebly contracted before the apex

Subg. *Dielis* Sauss. and Sichel; group of *C. pseudonyma*

7a. Longer hind tibial spur feebly contracted before the apex, i.e. somewhat spatulate

Subg. *Dielis* Sauss. and Sichel; group of *C. pseudonyma*

b. Longer hind tibial spur strictly acute

Xanthocampsomeris subg. nov.

8a. Without the combination of characters found in 8b ..... (9)

b. Terga 2 and 3, and in all but two species also 1 and 4, banded with yellow or orange, or entirely orange, or orange-red. Vestiture, except on the apical segments, entirely white or buff, or the ruff

around the neck rusty, the abdominal fringes sometimes coppery. Wings yellowish-hyaline, a little more infuscated beyond the cells, sometimes smoky throughout but not deeply so. Occiput and vertex polished and impunctate; longer hind tibial spur feebly spatulate; dorsal surface of the propodeum tending to culminate in a carina or sharp ledge which may overhang the posterior surface, but in some species this is reduced to only a median projecting point; the area horizontalis medialis closely punctate except for a small median impunctate triangle that terminates in the apical point of the ridge

Subg. *Campsomeriella* Betrem; group of *C. plumipes* (Drury)

9a. Posterior face of propodeum impunctate, or if strongly punctate, then only so above and the longer hind tibial spur spatulate (*regifica* and *atrata*). If any white vestiture is present, then the mesopleural ridge obsolete, the upper part of the lower plate and the upper plate impunctate and polished .....(12)

b. Posterior face of propodeum coarsely, rugosely, punctate throughout and bearing erect setae (the punctation of the posterior face of the propodeum is reduced in some *brasiliana,* but these forms may be recognized as coming here by the combination of white or fulvous tergal fringes and distinct mesopleural ridge and punctures); hind tibial spurs acute; white or fulvous vestiture frequent; the mesopleural ridge distinct, the plates punctate and hairy; first tergum always immaculate .....*Pygodasis,* subg. nov. (10)

10a. Color entirely black or tergum 2 with a pair of lateral flecks, or 2 and 3 orange red .....(11)

b. One or two terga spotted or banded with yellow or orange, but not with terga 2 and 3, and only those, orange-red; the spots or bands nude; wings dark or ferruginous .....Group of *C. quadrinotata* F.

11a. All vestiture black; wings stained ferruginous or somewhat orange, or deep blue-black with metallic reflection .....Groups of: *C. ephippium* (Say), *C. lucasia* (Sauss.), and *C. fallax* (Sauss.)

b. All vestiture, or at least some tergal fringes, white, sometimes long and dense; wings hyaline or stained yellowish

Group of *C. cineraria* (Sich.)

12a. Abdominal terga matt; scutellum, metanotum, dorsal and posterior faces of propodeum, some or all of them, punctate, not all smooth and polished .....(13)

b. Abdominal terga polished and shining; occiput, vertex, most of mesoscutum, scutellum, metanotum, area horizontalis medialis, and area posterioris, impunctate and polished. Black, with black vestiture and deeply infuscated violaceous wings (sometimes a fleck of yellow on the scutellum and post-scutellum)

Subgenus *Laevicampsomeris* Betrem

13a. Mesopleura with a distinct epicnemial ridge, or the upper plate with numerous punctures, or both; vestiture entirely black .....(15)

b. Mesopleural ridge weakly indicated and only just above the coxae, elsewhere wanting, the surface of the lower plate of the mesopleura polished and almost or quite impunctate, the upper plate smooth and rounded, like a water-worn pebble, impunctate and polished except for the dorsal surface of the low tubercle; first tergum with a yellow band or spots or all terga immaculate; white vestiture often present .....*Lissocampsomeris*, subg. nov. (14)

14a. Forewings with a pronounced costal fuscous bar; vestiture of pectus entirely black .....Group of *C. wesmaeli* (Lep.)

b. Forewings with at most a feebly darker costal bar, and if this is the case, then the vestiture of the pectus is white
Group of *C. argentea* (Hal.)

15a. Longer spur of hind tibiae sometimes acute, usually spatulate, from 0.68 to 0.8 of the length of the metatarsus; hypopygium rounded, the lateral processes small and spine-like, largely concealed by stiff bristles. Always entirely black ..Subg. *Campsomeris* Guérin (16)

b. Longer spur of hind tibiae acute, short and stout, 0.4 of the length of the metatarsus; hypopygium subquadrate with two heavy peg-like lateral teeth. Predominantly yellow to entirely black
Aeolocampsomeris, subg. nov.

16a. Longer hind tibial spur acute; wings usually hyaline
Stygocampsomeris, sect. nov.

b. Longer hind tibial spur spatulate; wings deeply infuscated, in *C. atrata* orange-yellow at base .....Sect. Campsomeris Guérin

17a. Apical spurs of the hind tibiae black, or if white, then tergal fringes all black (*C.* [*Pygodasis*] *fallax*), or all vestiture black .....(21)

b. Apical spurs of the hind tibiae white, the basal 3 or 4 tergal fringes white, vestiture never all black .....(18)

18a. Wing-membrane bare beyond the cells, unless along costal margin (19)

b. Wing-membrane uniformly hairy; a yellow band on tergite 4, and the vestiture on at least one of terga 4 to 7 pale, usually red (if tergum 4 is immaculate and the vestiture on terga 4–7 entirely black, confer variants of *C.* [*Lissocampsomeris*] *wesmaeli*)
Xanthocampsomeris, subg. nov.

19a. Fifth tergum not banded .....(20)

b. Fifth tergum with a yellow band; vestiture entirely white; scapulae each with a yellow spot
Subg. *Campsomeriella* Betrem; group of *C. pilipes* (Sauss.)

20a. Clypeus black, or with lateral margins entirely yellow; pronotum black or with a yellow band which usually extends to the tegulae
Subg. *Campsomeriella;* group of *C. plumipes* (Drury)

b. Clypeus with a yellow spot on each side; pronotum with a pair of lateral spots, rarely connected medially
Subg. *Dielis* Sauss. and Sich.; group of *C. pseudonyma* (Schulz)

21a. Wings beyond the cells bare, at least behind the line of the cubital vein as projected to the margin .....(23)

b. Entire wing-membrane beyond the cells hairy; wings never deeply infuscated ....(22)

22a. Usually heavily marked with yellow, if not, at least the sides of the clypeus yellow; at least some white vestiture on venter and legs
Lissocampsomeris subg. nov.; group of *C. wesmaeli* (Lep.)

b. Entirely black, with all vestiture black
Campsomeris Guérin; Stygocampsomeris, sect. nov.

23a. Propodeum and clypeus black .....(24)

b. A large median postero-lateral spot on the propodeum as well as entire clypeus yellow; vestiture nearly all white but inconspicuous; wings only slightly stained .....*Aeolocampsomeris,* subg. nov.

24a. Sternum 4 without an apical median area of minute dense punctulation and erect silky setae .....(25)

b. Sternum 4 with an apical area, at least medially, of minute dense punctulation bearing a brush of erect silky setae
Pygodasis, subg. nov.; group of *C. ephippium* (Say)

25a. Pale areas on tergites wanting, or bearing black setae .....(26)

b. Yellow or orange areas extensive on tergum 2, usually on t. 3, and sometimes on t. 1, but always clothed with pale fine setae
Pygodasis, subg. nov.; group of *C. quadrinotata* (F.)

26a. Apical wing-membrane bare except narrowly along the costal margin (27)

b. Apical wing-membrane hairy to the line of the cubital vein; wings brownish hyaline with a costal fuscous bar; three tergites with narrow interrupted apical yellow bands; scutellum with spots and metanotum with a yellow bar
Pygodasis, subg. nov.; group of *C. fallax* (Sauss.)

27a. Vestiture entirely black, the thorax entirely black .....(29)

b. At least some vestiture on the venter and on the legs white, or the scutellum and metanotum yellow .....(28)

28a. Five terga banded with yellow, or some only anteriorly, or none; vertex and dorsum black; vestiture long and silky, all white; wings hyaline ..... *Pygodasis,* subg. nov.; group of *C. cineraria* (Sich.)

b. Only three terga banded, the wings fuscous, the thorax spotted and the vestiture all black, or the abdomen entirely black, the wings only slightly stained, the thorax immaculate, and at least the vestiture of the apical four abdominal segments black
Pygodasis, subg. nov.; group of *C. ephippium* (Say)

29a. Tergum 2 without comma-shaped marks .....(30)

b. Tergum 2 with a pair of comma-shaped marks
Pygodasis, subg. nov.; group of *C. ephippium* (Say)

30a. Wings orange-hyaline; sometimes three terga banded
Pygodasis, subg. nov.; group of *C. lucasia* (Sauss.)

b. Wings deeply infuscated, but sometimes orange or hyaline basally; entirely black or with only terga 2 and 3 bearing narrow interrupted apical lines . .Subg. *Campsomeris* Guérin; sect. Campsomeris.

Subgenus CAMPSOMERIELLA Betrem

1928. Subgenus *Campsomeris* Betrem, Treubia, v. 9, suppl., p. 122; nec Guérin. (Incorrectly used here as though *Scolia thoracica* F. were the type-species.)

I. Group of *C. sauteri Betrem*. Indo-Australasian.
II. Group of *C. thoracica* (F.). Indo-Australasian, Palearctic, and Ethiopian.
III. Group of *C. dohrni* (Mantero). Indo-Australasian.
IV. Group of *C. marginella* (Klug). Indo-Australasian.

1941. *Campsomeriella* Betrem. Notes d'Entomologie chinoise, 8:86, n.n. for subg. Campsomeris Betr. '28, nec Guérin.

Type-species: *Scolia thoracica* Fabr. = *Campsomeris* (*Campsomeriella*) *thoracica* (Fabr.).

The spurs of the ♀ are black, of the ♂ white.

V. Group of *C. plumipes* (Drury)

♀. As described in the key, to which may be added that the mesopleura have a well-developed but not sharp ridge, sometimes feeble at the lower margin of the upper plate, considerably punctate and setiferous, and that the abdominal terga are matt.

♂. Very slender, black, terga 1-4 banded with yellow, clypeus yellow but usually black medially or only the sides yellow; hind tibial spurs white; vestiture entirely white; membrane of the front wings nearly devoid of hair beyond the cells.

This group is more primitive than any of the three Indo-Australasian groups recognized by Betrem in that the most primitive females retain the archetypal color pattern of the genus. But the oriental groups may well have been derived from these.

Distribution.—Austral North America to Chile and Argentina.

List of Species

1. *C. bahamensis* Bradley, 2. *C. chilensis* (Sauss.) n. comb. [= *similaris* Rohwer], 3. *C. dorsata* (Fabr.) Bradley, 4. *C. plumipes* (Drury) Viereck, 5. *C. tolteca* (Sauss.) Bradley, with var. *dives* (Prov.) Bradley, 6. *C. trifasciata* (Fabr.) Bradley [= *Scolia radula* F., *C. alexandri* (Lep.)], 7. *C. whitelyi* (Kirby) new combination.

VI. Group of *C. pilipes* (Saussure)

♀. Medium sized species. Black, terga 1-3 and sometimes 4 with wide yellow or orange-yellow bands which may occupy most of the terga. Vestiture white; the abdominal fringes in part yellow or coppery, or the

setae of the dorsum, vertex and face may be brown. Wings yellowish, more smoky towards the apex but not spotted, with a feeble violaceous lustre. Hind tibial spurs long, slender, feebly spatulate, testaceous. Scapulae with a feeble furrow close to the inner margin, and with a feeble, flattened, irregular, curved, transverse carina in front of the tegulae. Mesopleura with a moderately sharp ridge, ending above in a small tubercle. Area horizontalis medialis closely punctate except for a distinct median point merging roundly into the posterior face, the upper part of which is punctate; terga matt.

♂. Of the *plumipes* type, but the head and thorax with less yellow, the clypeus black or with lateral yellow spots.

Distribution.—Southwestern United States and northern Mexico.

List of Species

1. *C. pilipes* (Saussure) Bradley.

Subgenus DIELIS Saussure and Sichel

1864. Subgenus *Dielis* Sauss. & Sich. Cat. des Espèces de l'ancien genre *Scolia*, p 161.

1928. Subgenus Dielis Betrem. Treubia, v. 9, suppl., p. 87.

I. Group of *C. radula* (F.) Indo-Australasian.

II. Group of *C. annulata* (F.) Indo-Australasian.

Type-species: *C. radula* (F.). By designation of Betrem '28, p. 87.

Betrem's group III to VII have all now become other subgenera. Our American species, at least pending closer study of their relationship, may be allowed to constitute a third species group.

III. Group of *C. pseudonyma* (Schulz)

Distribution.—Brazil and Paraguay.

List of Species

1. *C. auripilis* (Fox) n. comb., 2. *C. pseudonyma* (Schulz) n. comb. [=*smithii* (Fox)].

XANTHOCAMPSOMERIS, subg. nov.

1928. (*Dielis*) Gruppe III. Betrem, Treubia, v. 9, suppl., p. 97.

Type-species: *Tiphia tricincta* Fabr.

I. Group of *C. aurulenta* (Smith)

This comprises the Indo-Australasian group called Group III of Dielis in Betrem's monograph. The species that comprise this group differ from the American species primarily in the characteristic form of the male genitalia; also the tergal bands show no tendency towards interruption, nor do they ever become very wide as in the *plumipes* group.

II. Group of *C. tricincta* (F.)

♀. Small to medium-sized species. In addition to the characters noted in the key: Punctation of head variable, the occiput and vertex sometimes almost impunctate, much as in *Campsomeriella,* sometimes entirely punctate, usually at least the upper median part of the occiput punctate; mesopleural ridge distinct, often carinate, not ending in a tubercle above; posterior face of propodeum usually impunctate, but sometimes with dense punctures above; dorsal surface of propodeum terminating in a ridge or merely a central point; punctation of the area horizontalis medialis fine and often obscured by pile, usually with a median tuft of setae; terga matt.

♂. Of the slender *plumipes* type, 3 or 4 terga banded with yellow, the vestiture short and white, but often red at apex of the abdomen, the legs in greater or lesser degree red; wings subhyaline, the veins yellow, the area beyond the cells densely hairy throughout, except in *limosa;* hind tibial spurs white.

In this subgenus, which comes close to *Campsomeriella*, group of *C. plumipes,* the color pattern differs in that there is a strong tendency for the tergal bands to be deeply divided, even when not fully interrupted, and red legs are usual, whereas in the *plumipes* group the bands show little tendency towards interruption, the median notch is usually broad and shallow or wanting, and the line of modification is for the bands to narrow or widen instead of breaking into two spots; the legs in that group are red in only one species.

Distribution.—Arizona to Colombia, and Florida to the West Indies.

List of Species

1. *C. completa* Rohw. (with ssp. *yucatanensis* Rohw.), 2. *C. fulvohirta* (Cress.) Rohw., 3. *C. hesterae* Rohw., 4. *C. limosa* (Burm.) Rohw., 5. *C. tricincta* (F.) Rohw. [= *pyrura* Rohw. = *undulata* (Sm.)].

RHABDOTOMERIS, subg. nov.

Type-species: [*Elis mexicana* Cameron, 1893] = *Campsomeris* (*Rhabdotomeris*) *rokitanskyi* (D.T.).

♀. Moderately large black species with a pair of large yellow spots, or an interrupted band, on terga 2 and 3. All setae black; white pile barely perceptible. Wings medium dark, with not strong violaceous reflection. Hind tibial spurs very long, piceous, slender and spatulate. Head matt, sloping behind the eyes, the vertex and occiput with moderate, coarse, but not dense punctures. Area horizontalis medialis projecting over the area posterioris, forming a ridge, but not sharply carinate, without a median point. Both surfaces very densely, confluently, and coarsely punctate throughout, especially the area horizontalis. Terga matt.

♂. Vestiture white or mixed with black; 3 or 4 terga banded with yellow; clypeus with lateral yellow spots; scapulae with yellow bars; scutellum with 2 fused spots; metanotum black.

Distribution.—Mexico to Ecuador.

List of Species

1. *C. rokitanskyi* (D.T.), n. comb. [= *mexicana* (Cam.)].

PYGODASIS, subg. nov.

Type: *Scolia quadrinotata* Fabr.

Large to very large species. Wings ranging from clear hyaline through yellowish hyaline and yellowish smoky to deeply infuscated and violaceous, never with a strong costal fuscous bar, and never with a preapical fuscous spot. The first tergum never maculate in the female, and only rarely so in the male; terga 2 and 3 with yellow or orange spots in primitive types. These spots become continuous, and in each sex of *ephippium* form an orange-red caparison for each of these terga; in other species they are entirely lost, the color being then wholly black, as thoracic or facial maculation does not occur in either sex, except for clypeal flecks in *quadrinotata*. The entire vestiture may be white, is sometimes mixed, but more usually wholly black. The tibial spurs always acute, not exceptionally long, and always black in each sex. The males less slender in comparison to the females than are those of the subgenera *Campsomeriella* and *Dielis*, and in the more specialized types (*cineraria* and *ephippium*) as stout as the females, which they may (*ephippium*) very closely resemble.

Distribution.—Austral U.S. to Argentina.

I. Group of *C. quadrinotata* (F.)

Distribution.—Southeastern U.S., ? Jamaica; Panama and Colombia; Bolivia, Paraguay, and Brazil to Argentina and Uruguay.

List of Species

1. *C. bistrimaculata* (Lep.), n. comb. [=*fossor* (Sauss.), *talpa* (Sauss.)], 2. *C. quadrimaculata* (F.), Viereck * [=*Vespa maculata* Drury, *C. druryi* Cockerell], 3. *C. quadrinotata* (F.) Lepeletier, 4. *C. terrestris* (Sauss.), n. comb. [=*bivittata* Kby., *consularis* (Burm.), *mutanda* (Sauss.), *vidua* (Sauss.)], 5. *C. vittata* (Sichel), n. comb. [=*argentina* (Brethes)] with ssp. *banksi* Bradley.

II. Group of *C. ephippium* (Say)

Distribution.—Texas to Ecuador and Argentina.

List of Species

1. *C. ephippium* (Say) Bradley, with ssp. *wagneriana* (Sauss.) Bradley, 2. *C. ianthina* Bradley, 3. *C. spegazzini* (Brethes), n. comb. [=*C. bruchi* (Brethes), n. synon.].

III. Group of *C. cineraria* (Sichel)

Distribution.—Brazil and Paraguay to Uruguay. All species are rare.

List of Species

1. *C. cineraria* (Sichel), n. comb., 2. ? *C. vernoniae* (Schrottky) n. comb. [=*C. cineraria* Fox, nec Sichel], 3. *C. vespiformis* (Sauss.), n. comb.

IV. Group of *C. lucasia* (Sauss.)

Distribution.—Colombia and Venezuela to Uruguay and Argentina.

List of Species

1. *C. colombiensis* Bradley, 2. *C. cristata* Bradley, 3. *C. lucasia* (Sauss.) Bradley.

V. Group of *C. fallax* Sauss.

Distribution.—Colombia and British Guiana to northern Argentina.

List of Species

1. *C. fallax* (Sauss.) Bradley, 2. *C. nigrans* Bradley. These are presumed to be the two sexes of one taxonomic species.

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* This species, described as from Jamaica, is unknown from that island, at least in recent years. It may be a subspecies of what is here termed *C. quadrinotata* (F.), or it may be an earlier name for that species, a matter not presently determinable.

AELOCAMPSOMERIS, subg. nov.

Type-species: *Campsomeris costalis* Lepeletier.

♀. Very large, with entirely black vestiture; easily recognizable by their short black hind tibial spurs. Head and thorax always wholly black; abdomen black, or the first tergum spotted or banded and terga two and three spotted. Wings hyaline, hyaline with a fuscous costal border, yellow, or uniformly dark. Area horizontalis medialis forming a projecting point.

♂. Large and moderately stout, but less so than the female. Vestiture white, the tibial spurs black. More heavily marked with yellow than are the females; terga 1 to 5 banded, the bands interrupted on 2 to 5, the clypeus, united scapulae, scutellum, metanotum, area horizontalis medialis, lateral corners of propodeum, and spots and stripes on the pleura and legs, all yellow. Wings hyaline, their membrane bare beyond the cells.

Some reduction of the typical male coloration occurs.

Distribution.—Mexico to Rio Grande do Sul.

List of Species

1. *C. brethesi* (Bradley) Bradley, 2. *C. campestris* (Brum.), n. comb. [=*pulchella* (Sauss.)], 3. *C. variegata* (Fabr.) Lep. [=*fuscata* (Klug), *costalis* Lep., *lativentris* (Sauss.), *irregularis* (Smith)], with var. *lucida* Lep.

Subgenus CAMPSOMERIS Guérin

Type-species: *Scolia atrata* Fabr., by designation of Bequaert, 1926, Ent. Mitt., 15: 190.

Very large wasps, entirely black, with black vestiture.

♀. Longer hind tibial spur from 0.68 to 0.8 of the length of the metatarsus. Hypopygium rounded, the lateral processes small and spine-like, largely concealed by stiff bristles.

Distribution.—West Indies, Guatemala to northern Argentina and Chile.

Section CAMPSOMERIS Guérin

1838. Subgenus *Campsomeris* Guérin, p. 247. (*In* Duperry, Louise Isidore. Voyage autour du Monde . . . sur la Corvette de S.M. la Coquille. Paris. Zool. v. 2, pt. 2.) Type-species: *Scolia atrata* Fabr., by designation of Bequaert, 1926, p. 190.

1845. *Colpa* Lepeletier. Hist. nat. des insectes. Hyménoptères. v. 3, p. 534. Type-species: *Colpa peregrina* Lep. by designation of Betrem, 1928.

♀. Wings dark violaceous, or basally orange (*atrata*). Longer spur of the hind tibia spatulate, occasionally not so.

♂. Wings dark violaceous, orange (*atrata*), or with the basal half abruptly and entirely hyaline (*vitripennis*).

Distribution.—West Indies; Costa Rica to Argentina.

List of Species

1. *C. atrata* (Fabr.) Bequaert, 2. *C. peregrina* (Lep.) Bradley, 3. *C. regifica* Bradley, 4. *C. vitripennis* (Smith).

STYGOCAMPSOMERIS, sect. nov.

Type-species: *Scolia servillei* Guérin.

♀. Posterior tibial spurs black, acute.

Distribution.—Guatemala to n. Argentina and Chile.

List of Species

1. *C. corrigenda* (Schulz), n. comb. [=*nigra* (Sauss.)], 2. *C. sanctae-theresae* Bradley, 3. *C. servillei* (Guérin) Bradley, [=*hyalina* Lep.,=*neotropica* Grib.].

LISSOCAMPSOMERIS, subg. nov.

Type-species: *Colpa wesmaeli* Lepeletier.

Small to medium-sized species with black tibial spurs. Wings yellowish hyaline, in two species with a fuscous costal bar, and in two other species deeply infuscated with strong reflection. Vestiture varying from entirely black to more or less white.

♀. Black, with a maximum pattern of yellow markings consisting of a bar or pair of spots on the first tergum, and a pair of spots on each of terga 2 and 3. Of these, those on tergum 3 are first to disappear, followed by those on tergum 2, then those on tergum 1, until the resulting body-color is entirely black. The tibial spurs black, the longer hind one varying from slightly to strongly spatulate; the area horizontalis medialis coarsely punctate, with a median, impunctate, polished, triangle that ends in a projecting point, which may be widened to form an overhanging ridge.

♂. Wing-membrane beyond the cells hairy throughout. In *C. wesmaeli* the primitive coloration of the males begins with the basal three abdominal terga banded, the thorax also considerably marked with yellow, but they lose this coloration and in some species are wholly black, and very like the females in form and size. The segments of the abdomen slender as in *C.* (*Campsomeriella*) *plumipes*.

Distribution.—Mexico and the Guianas to Argentina.

List of Species

1. *C. argentea* (Hal.), n. comb. [= *brasiliana* (Sauss.), *gerstaeckeri* (Sauss.)], 2. *C. aureohirta* (Fox), n. comb., with ssp. *ecuadorensis* (Cam.) n. comb., 3. *C. columba* (Sauss.) Bradley, with ssp. *albofimbriata* (Smith) Bradley, 4. *C. hoffmannseggii* (Klug) Bradley [= *hexaspilota* (Spin.), *ambigua* (Sichel), *klotzii* (D.T.)], 5. *C. idonea* Bradley, 6. *C. wesmaeli* (Lepeletier) Bradley [= *conformis* (Spin.), *conspicua* (Smith)].

Subgenus LAEVICAMPSOMERIS Betrem

1928. Subgenus *Dielis* Betrem. Treubia, v. 9, suppl., p. 105 & 107.
IV. Group of *C. nigerrima* Smith. Indo-Australasian
1933. Subgenus *Laevicampsomeris* Betrem. Stett. Ent. Zeit. 94:238.

Type-species: *Scolia nigerrima* Smith.

♀. Large species. Polished, shining and with few punctures, but in some oriental species much more punctate. Temporal ridge strong, at some distance behind the eyes, the occipital surface declining but little so that the occipital carina is clearly visible from a dorsal view. Scapulae rather finely and densely punctate, with a feeble furrow (strong in some oriental species) close to the inner margin, broad posteriorly, and with a curved carina setting off a smooth area in front of the tegulae; mesopleural ridge well marked but not sharp on the lower plate, which is punctate and setose, feeble on the upper plate which is strongly punctate and setose except on the lower margin and which forms a pronounced tubercle above meeting the scapular lobe (the ridge feeble in some oriental species, the mesopleura nearly impunctate, and the tubercle not distinct). Hind tibial spurs black, long and slender, and spatulate.

♂. Males are not known in America. Indo-Australasian males are blue-black with a metallic lustre; black vestiture with fine appressed silvery pile; moderately dark wings more deeply infuscated along the costal border, the membrane beyond the cells bare except along the costal margin; tibial spurs black.

Habitat: Brazil.

List of American Species

1. *C. tenebricus* Bradley.

SPHENOCAMPSOMERIS, subg. nov.

Type-species: *Dielis obesa* Sauss., 1869.

♀. Large black species; terga 2 and 3 each with a pair of orange spots. All setae black, but head, altitrunk, and first sternum with appressed silvery pile. Wings dark with violaceous reflection. Head broadly rounded

behind the eyes, somewhat bullet-like, polished, the vertex and occiput with sparse, fine, punctures. Scapulae full, rounded, not furrowed, a curved, transverse, carina in front of each tegula. Mesopleura with a strong but not sharp ridge, not ending above in a strong tubercle. Area horizontalis medialis and area verticalis medialis both closely finely and uniformly punctate, meeting somewhat abruptly but not in a sharp carina, the former projecting somewhat over the latter, but not forming a median point. Terga shining.

♂. The males large and very stout, not disimilar to the female in form. Abundantly marked with yellow. The vestiture short and white.

Distribution.—Brazil and Argentina. Rare.

List of Species

1. *C. obesa* (Sauss.), n. comb.

STUDIES ON THE LARVAE OF DIGGER WASPS (HYMENOPTERA, SPHECIDAE) PART III: PHILANTHINAE, TRYPOXYLONINAE, AND CRABRONINAE[1]

BY HOWARD E. EVANS

Cornell Universtiy, Ithaca, N. Y

(Plates IX to XX)

This is a continuation of a series of papers begun by Evans and Lin.[2] The subfamilies Philanthinae, Trypoxyloninae, and Crabroninae are considered together here merely as a matter of convenience. The Philanthinae are most certainly not closely related to the other two, although the Trypoxyloninae and Crabroninae actually have many characters in common and are probably closely related. This problem, along with other matters concerning the classification of the Sphecidae, will be considered in the final paper of this series. The reader is referred to Part I for a discussion of techniques and terminology.

SUBFAMILY PHILANTHINAE

I have studied larvae of all Nearctic genera of this subfamily with the exception of *Trachypus*, which is doubtfully recorded from the Southwest. The larvae of Philanthinae are immediately separable from all other Sphecidae by the densely spinulose integument, the slender mandibles, and the conical or tubular anal segment. The tribes and genera of Philanthinae are quite distinct and readily separable.

Characters of the subfamily.—Body fusiform, the posterior end conically protuberant, either the supra-anal or the subanal

[1] Acknowledgement is made to the Grace H. Griswold Fund of the Entomology Department of Cornell University for assuming the cost of engraving the plates. Many of the larvae described here were collected in the course of studies on the comparative ethology of digger wasps, a project supported by the National Science Foundation.

[2] Part I: Sphecinae. Trans. Amer. Ent. Soc., 81: 131-153, pls. I-VIII. January 1956. Part II: Nyssoninae. Trans. Amer. Ent. Soc., 82: 35-66, pls. II-XIV. August 1956.

lobe projecting, or the two lobes together forming a tubular projection; integument nearly everywhere with a dense covering of minute, slender spinules; body setae, when present, not abundant and not projecting above these spinules; spiracles with the peritreme not clearly defined, the walls of the atrium divided into hexagons by a network of non-spinose ridges, the opening between the atrium and subatrium simple, circular, unarmed. Head higher than wide; coronal suture strong; parietal bands absent; antennal orbits circular or nearly so, the antennal papilla present, of variable length; head with scattered setigerous punctures, the setae generally very small; epistomal suture weak. Labrum with numerous punctures, from some of which may arise fairly strong setae; margin of labrum with or without conical sensilla and at most weakly spinose or setose; epipharynx variously spinulose and papillose, the sensory areas bare, usually unpigmented; mandibles slender, acuminate, more than twice as long as wide at the base, the apex with two or three teeth (a weak fourth tooth in *Aphilanthops*), the base laterally with one or a few minute setae; maxillary palpi strong, galeae much smaller than the palpi, either very short, hardly longer than broad, or at least very slender and much shorter than the palpi; lacinial area papillose, spinulose, or both; spinnerets paired, either short and blunt or longer, acute, horn-shaped, but in any case not more than 1.5 times the length of the labial palpi; oral surface of the prementum strongly papillose.

Table of Tribal and Generic Characters

A. Mandibles tridentate or weakly quadridentate (figs. 5, 12); epipharynx spinulose or papillose over most of its surface (figs. 4, 14); spinnerets blunt, not longer than the labial palpi (fig. 8) PHILANTHINI

B. Mandibles weakly quadridentate (fig. 5); lacinial area more or less papillose and with a finger-like process (fig. 9); labrum without conspicuous setae (fig. 4); subanal lobe conically produced (fig. 3) ..... *Aphilanthops* (*frigidus*)

BB. Mandibles tridentate (fig. 12); lacinial area densely spinulose, without a finger-like process (fig. 11); labrum with numerous strong setae (figs. 14, 16); anal segment tubular, the subanal lobe not protuberant (fig. 13)
Philanthus (*gibbosus, solivagus, bilunatus, politus,* [*triangulum*])

AA. Mandibles bidentate (fig. 29); epipharynx with a considerable area medio-basally which is devoid of spinules or papillae (figs. 30, 31, 34); spinnerets horn-shaped, often surpassing the labial palpi (fig. 26) .....CERCERINI

B. Head slightly higher than wide, somewhat elliptical in anterior view (fig. 22); anal segment with the supra-anal lobe surpassing the subanal (fig. 23); galeae slender, fairly long, usually about half the length of the maxillary palpi (fig. 21)
Cerceris (*fumipennis, nigrescens, robertsonii, clypeata, angularis,* [*rubida julii, quinquefasciata*])

BB. Head very much (about 1.5 times) higher than wide, more or less parallel-sided (fig. 32); anal segment tubular, the supra-anal and subanal lobes about equally prominent (fig. 33); galeae very minute (fig. 35) .....*Eucerceris* (*flavocincta*)

Tribe Philanthini

Aphilanthops frigidus (Smith) (Plate IX, figs. 1-10)

Body.—Length 12 mm.; maximum width (abdominal segment 5) 3.8 mm. (fig. 3). Strongly fusiform; pleural lobes moderately prominent, rounded; dorsal annulets feebly developed, but each abdominal segment crossed by a narrow, rather inconspicuous transverse elevation about midway of its length. Integument everywhere strongly and rather densely spinulose (fig. 7), without setae except for a few small ones intermingled with the spinules and scarcely longer than these; spinules slightly longer and more darkly pigmented along the transverse elevations and down onto the pleural lobes. First thoracic segment impressed medio-dorsally. Supra-anal lobe moderately prominent; subanal lobe strongly, conically produced. Spiracles all about the same size, the second thoracic spiracles somewhat below the line formed by the other spiracles. Spiracular peritremes unpigmented and weakly defined; atria lined with an irregular network of ridges; opening between atria and subatria small, simple, unarmed; subatria constricted and then abruptly expanded to the width of the tracheae (fig. 10).

Head.—Slightly higher than wide, measuring .8 mm. wide and .83 mm. high (figs. 1, 2). Pale straw-colored, only the apices of the mandibles conspicuously darker. In lateral view, the front is prominent and the clypeus strongly declivous; there are paired depressions in the middle of the front. Coronal suture strong, short; parietal bands absent. Antennal orbits 80 μ in diameter; antennae short, about 40 μ long and 30 μ wide at the base, capped by three conical sensilla (fig. 6). Head capsule with a few widely scattered, minute, setigerous punctures; clypeus somewhat more densely punctate.

Mouthparts.—Labrum strongly bilobed and deeply emarginate; width .36 mm.; maximum height .13 mm. (fig. 4). Surface of labrum with scattered small punctures which grade into sensilla along the apical margin;

margin roughened and rather spinose on the anterior lateral corners. Epipharynx with the sensory areas well defined but unpigmented, each containing about six pores; there are also a few additional pores basad of these among the spinules; greater part of the surface covered with short, stout spinules which grade into papillae basad and laterad. Mandibles .42 mm. long and .20 mm. wide at the base; apex acute and inner margin with two additional teeth and a poorly defined fourth tooth; base with a few minute setae laterally (fig. 5). Maxillae strongly papillose, the lacinial area with a short, finger-like projection; palpi 75 μ long and about 35 μ wide at the base; galeae about 18 μ long and nearly as wide (fig. 9). Labial palpi 35 μ long and 28 μ wide at the base; spinnerets paired, unpigmented and inconspicuous, slightly shorter than the palpi (fig. 8).

Material.—Described from 16 specimens from Ithaca, New York, July 20-Aug. 24, 1955-56 (C. S. Lin, H. E. & M. A. Evans).

Philanthus gibbosus (Fabricius) (Plate X, figs. 11-15)

Body.—Length 13 mm.; maximum width 4 mm. (fig. 13). Form similar to *Aphilanthops,* but a little more slender, and without any evidence of the transverse elevations on the dorsum. Integument with rather uniformly distributed spinules much as in *Aphilanthops.* Anal segment in the form of a truncated cone, the supra-anal and subanal lobes about equally developed. First thoracic spiracles slightly larger than the others; second thoracic spiracles slightly below the line formed by the other spiracles. Spiracular atrium lined with ridges forming regular hexagons; opening between atrium and subatrium simple, small, the subatrium gradually enlarged from the opening (fig. 15).

Head.—Slightly higher than wide, measuring .75 mm. wide and .85 mm. high. Shape and features very much as described and figured for *Aphilanthops frigidus;* front and clypeus, in lateral view, somewhat less prominent. Antennal orbits 75 μ in diameter; antennae short, conical, about 35 μ in length.

Mouthparts.—Labrum bilobed and with a broad apical emargination; width .39 mm.; maximum height .15 mm. (fig. 14). Surface of labrum with scattered punctures, most of which bear setae, and roughened with small papillae which become more dense anteriorly. Epipharynx spinulose, the sensory areas unpigmented and devoid of spinules, each with about five pores. Mandibles .43 mm. long and .19 mm. in maximum width; apex acute and inner margin with two additional, somewhat rounded teeth; base with one small seta laterally (fig. 12). Maxillae apically strongly papillose, the lacinial area densely spinulose, the spinules set off sharply from the papillae; palpi 70 μ long; galeae very small, about 10 μ long and about as wide (fig. 11). Labial palpi 40 μ long; spinnerets slightly shorter than the palpi but arising from a slight elevation and extending about as far as the palpi; surface of the labium strongly papillose.

Material.—Seven specimens from Ithaca, N. Y., Sept. 1954 (C. S. Lin); two specimens from cocoons collected in Woodstock, Maryland (E. G. Reinhard) [U. S. Nat. Mus.].

Philanthus solivagus Say (Plate X, figs. 16-18)

Body.—Length 13 mm.; maximum width 4 mm. In all respects very similar to *P. gibbosus.*

Head.—Width .72 mm.; height .82 mm. Antennal orbits 65 μ in diameter, the antennae only about 25 μ long (fig. 17). In all other respects as described for *gibbosus.*

Mouthparts.—Labrum .39 mm. wide, .16 mm. in maximum height (fig. 16); similar to *gibbosus* but with several distinct barrel-shaped sensilla near the outer apical angles. Epipharynx spinulose, the spinules becoming larger laterad and grading into papillae basad; sensory areas each with six pores. Mandibles .45 mm. long and .19 mm. in maximum width; apex tridentate and base with one small seta laterally, as in *gibbosus.* Maxillae about as in *gibbosus,* the spinulose area on the lacinia apparently slightly larger and composed of smaller spinules; palpi 80 μ long; galeae 10 μ long (fig. 18). Labial palpi only about 30 μ long, with several setae near them.

Material.—Six specimens from Ithaca, N. Y., Sept. 1954 (C. S. Lin).

Philanthus bilunatus Cresson (Plate XI, fig. 19)

Body.—Length 12 mm.; maximum width 3.6 mm. In all respects very similar to *gibbosus.*

Head.—Width .7 mm.; height .8 mm. Antennal orbits 80 μ in diameter, the antennae 35 μ long. Setigerous punctures somewhat more abundant and conspicuous than in *gibbosus.*

Mouthparts.—Labrum .36 mm. wide, .14 mm. in maximum height; apical margin with about six clearly distinguishable barrel-shaped sensilla on each side of the median line (fig. 19). Epipharynx with two sensilla on each side of the median line at the sides of the emargination, otherwise similar to the preceding two species except in minor details as figured. Mandibles .42 mm. long and .19 mm. in maximum width, tridentate and unisetose, exactly as figured for *gibbosus.* Maxillae broad apically, the lacinial area broadly spinulose as in the preceding species, the spinules set off sharply from the papillae; palpi 70 μ long; galeae 15 μ long. Apex of the labium strongly papillose; palpi 40 μ long and the spinnerets of about the same length.

Material.—Four specimens from Ithaca, N. Y., July 24-Aug. 10, 1954 (C. S. Lin).

Philanthus politus Say (Plate XI, fig. 20)

Body.—Length 12 mm.; maximum width 4 mm. No noticeable differences from the preceding three species.

Head.—Width .66 mm.; height .75 mm. Antennal orbits circular, 65 μ in diameter; antennae 35 μ in length. Head with abundant punctures bearing short setae.

Mouthparts.—Labrum .33 mm. wide, the apical margin with the usual emargination and with five clearly distinguishable barrel-shaped sensilla on each side (fig. 20). Epipharynx differing from *bilunatus* in having three sensilla on each side medio-apically and in having the sensory pores more numerous and more widely scattered. Mandibles .37 mm. long and .16 mm. wide, about as figured for *gibbosus* except that the number of setae on the base appears to vary from one to three. Maxillae about as in the preceding species; palpi 70 μ long; galeae exceedingly small, barely visible above the papillae. Labial palpi about 35 μ long, the spinnerets protruding to about the same length.

Material.—Three specimens from Ithaca, N. Y., June-July 1955 (H. E. Evans).

Philanthus triangulum Fabricius

The larva of this well-known Palaearctic species has been described and figured in detail by Grandi (1931, Boll. Lab. Ent. Bologna, 4: 37-43). In every respect it is very similar to the known North American species. The labrum bears three or four conical sensilla on each side of the median line much as in *politus*; the epipharynx also has a similar series near the apical margin; the sensory areas are small, apparently pigmented, and have about six pores in a small group. The mandibles have a single seta near the base laterally.

Tribe Cercerini

Cerceris fumipennis Say (Plate XI, figs. 21-26)

Body.—Length 15 mm.; maximum width (abdominal segment 4) 4.2 mm. (fig. 23). Fusiform; pleural lobes very prominent; anal segment conical, the supra-anal lobe prominent, protruding well beyond the subanal lobe. Each body segment with an oval area on each side of the middorsal line and a similar area on each pleural lobe; these areas are smooth and shining, devoid of spinules, and very slightly elevated. Integument elsewhere densely clothed with small spinules as in *Aphilanthops* and *Philanthus*. Spiracles small, virtually unpigmented; atrium lined with ridges forming more or less regular hexagons; opening into the subatrium small, unarmed; subatrium constricted, then abruptly expanded to the width of the trachea (fig. 24).

Head.—Considerably higher than wide, measuring 1.2 mm. high and 1.1 mm. wide (fig. 22). Pale straw-colored, the antennae, palpi, and galeae light brown; mandibles light brown at base, the apical half darker; anterior tentorial arms with an elongate brown spot apically and the pleurostomal thickenings with a brown spot just above the mandibular bases. Antennal orbits circular, about 90 μ in diameter; antennae moderately long, about 45 μ long and 25 μ in maximum diameter. Coronal suture rather long, unpigmented; parietal bands absent. Head with numerous small punctures, from a few of which arise minute setae.

Mouthparts.—Labrum .5 mm. wide; surface with scattered punctures, many of which bear setae; apical margin with about nine large conical sensilla on each side of the median emargination (fig. 25). Epipharynx apically with dense, small spinules which are directed inward; a large part of the central area of epipharynx is bare; about six sensory pores are present on each side. Mandibles .65 mm. long, .32 mm. in maximum width; base with about eight minute setae laterally; apex slender, the tip subacute and the inner margin with a single tooth somewhat back from the apex (about as illustrated for *nigrescens,* fig. 29). Maxilla with the lacinial area densely clothed with spinules over a broad area, the outer margin only rather weakly papillose; palpus 110 μ long, 40 μ in maximum thickness; galea slender and moderately long, about 55 μ long and 25 μ in maximum thickness (fig. 21). Labial palpus 75 μ long; spinnerets strongly protruding, horn-like, measuring about 90 μ; oral surface of labium strongly papillose (fig. 26).

Material.—One specimen collected by the author on the north bank of the Arkansas River, Arkansas Co., Ark., June 8, 1956.

Cerceris nigrescens Smith (Plate XII, figs. 27-29)

Body.—Length 14 mm.; maximum width 3.5 mm. Very similar to the preceding species; the two pairs of smooth welts on each segment seem to be smaller and less conspicuous.

Head.—Width 1.05 mm.; height 1.15 mm. Coloration as in *fumipennis,* the brown spots at the bases of the mandibles and the ends of the anterior tentorial arms conspicuous. Antennal orbits elliptical, 100 μ in maximum diameter; antennae 55 μ long and 23 μ in maximum thickness (fig. 28). Head capsule more sparsely punctate than in *fumipennis,* but with more of the punctures bearing short setae, especially on the clypeus.

Mouthparts.—Labrum .48 mm. wide, similar to that of *fumipennis*; epipharynx with a large area medio-basally which is devoid of spinules (fig. 27). Mandibles .7 mm. long, .3 mm. wide at the base; base with four small setae laterally; apex bidentate (fig. 29). Maxillae much as figured for *fumipennis*; palpi 100 μ long, galeae much more slender, about 55 μ long. Labial palpi 70 μ long; spinnerets elongate, horn-shaped, measuring 80 μ from the base.

Material.—One specimen from Ithaca, N. Y., July 15, 1955 (M. A. Evans).

Cerceris robertsonii Fox (Plate XII, fig. 30)

Body.—Length about 17 mm. Form similar to *fumipennis,* the dorsal and pleural welts unusually large and prominent.

Head.—Width 1.05 mm.; height 1.2 mm. Antennal orbits nearly circular, about 100 μ in diameter; antennae 60 μ long. In other respects as described for *fumipennis.*

Mouthparts.—Labrum .48 mm. wide, differing from the preceding two species in having a somewhat greater number of setae scattered over the surface and in having the margin somewhat more spinulose; epipharynx with three conical sensilla on each side of the median emargination (fig. 30). Mandibles as figured for *nigrescens,* measuring .65 mm. long and .28 mm. wide at the base. Maxillae and labium much as figured for *fumipennis*; maxillary palpi 105 μ long; galeae 55 μ long; labial palpi 85 μ long; spinnerets horn-shaped, about twice as long as the labial palpi.

Material.—Four specimens from Kill Devil Hills, Dare Co., N. C., July, 1950, collected by K. V. Krombein in connection with biological studies which have since been published (1952, Wasmann Jour. Biol., 10: 288-294).

Cerceris clypeata Dahlbom (Plate XII, fig. 31)

Body.—Length 13 mm.; maximum width 4.5 mm. Available larvae all in diapause, but agreeing well in most characters with the preceding three species. Smooth welts on each side of the mid-dorsal line and on the pleural lobes very large and prominent. Apex of the abdomen conically elongated, the supra-anal lobe projecting well beyond the subanal.

Head.—Width 1.35 mm.; height 1.55 mm. Features as in *fumipennis,* except the antennae more elongate, about 70 μ in length; antennal orbits nearly circular, 90 μ in diameter.

Mouthparts.—Labrum .68 mm. wide, the apical margin sinuate but not deeply emarginate, the surface provided with numerous setae, the margin provided with a series of small sensilla, about eight on each side (fig. 31). Epipharynx with three sensilla near the apical margin on each side of the median line; lateral apical portions with numerous spinules which are directed basad. Mandibles .9 mm. long, .4 mm. wide at the base, about as figured for *nigrescens.* Maxillary palpi 130 μ long; galeae slender, about 50 μ long; labial palpi 100 μ long; spinnerets horn-shaped, acute, diverging, somewhat shorter than the labial palpi.

Material.—Three specimens from cocoons collected at Pittsford, N. Y., July 30, 1955 (H. E. & M. A. Evans).

Cerceris angularis Cockerell

Williams (1919, Hawaiian Sugar Planters' Assoc. Exp. Sta. Bull., Ent. Ser., no. 14, pp. 146-148) has briefly described the larva of this Oriental species. The body form is apparently very similar to that of the North American species, the abdomen terminating conically with the supra-anal lobe more prominent than the subanal. The full-grown larva is said to be 28 mm. in length. Slide mounts of the head capsule and anterior part of the body, prepared by Williams, have been loaned to me by the Sugar Planters' Experiment Station. The integument has the usual dense covering of small spinules, and the spiracles are much as figured for *fumipennis*. A description of the head and mouthparts follows.

Head.—Much higher than wide, measuring about 1.2 mm. wide and 1.7 mm. high. Antennal orbits circular, 120 μ in diameter; antennae rather short, about 60 μ in length. Small setigerous punctures are present on the head capsule, but they are very sparse and inconspicuous.

Mouthparts.—Labrum with numerous setae; labrum and epipharynx with an unusual number of rather strong sensilla toward the apical margin, apparently about 15 on each side. Mandibles bidentate, the inner tooth rather blunt, perhaps from wear. Maxillary palpi 130 μ long; galeae slender, 60 μ long; labial palpi 110 μ long; spinnerets horn-shaped, diverging, about as long as the labial palpi.

Material.—Two head capsules and the anterior half of one larva, mounted in balsam, collected at Los Baños, Philippines, in 1917 (F. X. Williams).

Cerceris rubida julii Fabre

The larva of this Palaearctic species has been described briefly by Grandi (1926, Boll. Lab. Zool. Portici, 19: 288-290). The body is densely clothed with minute spinules as in the American species, and the head capsule bears rather numerous short setae. The labrum is not described in detail, but apparently bears numerous setae. The mandibles are bidentate as in the American species, and the maxillary palpi longer and stouter than the galeae. The spinnerets are horn-shaped, diverging, and considerably longer than the labial palpi.

Cerceris quinquefasciata Rossi

Grandi (1928, Boll. Lab. Ent. Bologna, 1: 279-285) has described in great detail the first, second, and final instars of this European species. The mature larva agrees very closely with the North American species in all but a few details. The shape of the head is somewhat unusual, the sides being bulging and the height barely greater than the maximum width. The maxillary palpi are unusually stout and the galeae very short and thick, almost as in *Philanthus*. The details of the labrum and epipharynx are very much as in *Cerceris robertsonii*. The spinnerets are horn-shaped and diverge sharply from the base.

Eucerceris flavocincta Cresson (Plate XII, figs. 32-35)

Body.—Length 18 mm.; maximum width 4.5 mm. Fusiform; pleural lobes fairly prominent; integument wholly clothed with small spinules and without the smooth areas dorsally and laterally characteristic of *Cerceris*. Anal segment conically protuberant, the supra-anal and subanal lobes about equally prominent (fig. 33). Spiracular atria lined with ridges forming small hexagons; all details of the spiracles very much as figured for *Cerceris fumipennis* (fig. 24).

Head.—Very much higher than wide, measuring 1.3 mm. high and only .83 mm. in maximum width (fig. 32). Pale straw-colored, with considerable brown blotching on the top and sides, especially around the coronal suture; labrum, mandibles, antennae, and pleurostomal thickenings brown; apical portion of the maxillae dark brown. Coronal suture rather long; parietal bands absent. Antennal orbits large and situated rather low; orbits circular, about 100 μ in diameter; antennae slender, rather long, about 60 μ in length and reaching the rim of the orbit when appressed. Head capsule with only small, inconspicuous setae.

Mouthparts.—Labrum .48 mm. wide; apical margin more or less rounded, with a weak median emargination; disc with numerous short setae and with a series of barrel-shaped sensilla toward the apical margin (fig. 34). Epipharynx similar to *Cerceris*, but the sensory areas somewhat pigmented and with the pores very weak; median apical part spinulose and with two large sensilla on each side. Mandibles in general similar to *Cerceris*, with several weak setae on the sides toward the base, the apex acute and the inner margin with a single additional tooth; length .65 mm, maximum width .25 mm. Maxillae with the palpi very large and prominent, 100 μ long and about 35 μ in maximum width; galeae minute, about 20 μ long and nearly as wide; lacinial area densely spinulose (fig. 35). Labial palpi 90 μ in length; spinnerets horn-shaped, acute apically, barely surpassing the palpi; oral surface of prementum papillose. In general, the apex of the labium resembles that of *Cerceris fumipennis* (fig. 26) except for slightly shorter spinnerets.

Material.—Six specimens from Independence, Sierra Co., Calif., 20 July 1954 (R. M. Bohart and J. A. Powell). These were collected in connection with biological studies which have now been published (1956, Pan-Pac. Ent., 32: 143-144).

Subfamily Trypoxyloninae

Larvae of this subfamily are rather commonly collected, as some of the species build mud nests and others nest in hollow twigs and other natural cavities. Larvae of Trypoxyloninae are easily distinguished from other Sphecidae by the ventral, preapical anus, the angulate lobe on the inner margin of the maxilla, and the characteristic mandibles. There is relatively little variation in larval form within the subfamily, and the genera and subgenera are separable only on rather minor characters. I have studied material of all three Nearctic genera and subgenera.

Characters of the subfamily.—Body somewhat cylindrical; pleural lobes prominent on the thorax and the first nine abdominal segments; posterior annulets more prominent than the anterior annulets; anus situated ventrally well before the apex of the last abdominal segment, which is produced in the form of a rounded or somewhat conical lobe; integument smooth; body with a few small, inconspicuous setae on the thoracic dorsum and often also on the pleural lobes and the last abdominal segment; spiracles with the atrium simple, the walls not lined with strong ridges or other armature; opening between the atrium and subatrium simple, unarmed; subatrium elongate. Head wider than high; parietal bands very weak or absent; epistomal suture distinct; antennal papilla absent, the three sensilla arising from the membrane of the orbit; head with numerous rather prominent setae, most abundant on the lower sides. Labrum with several large setae on the disc and several others on the apical margin medially, the margin sometimes with minute sensilla but never with well-defined barrel-shaped sensilla; epipharynx rather sparsely spinulose, without well-defined sensory areas, with or without a group of small sensory pores or cones on each side; mandibles large and stout, always somewhat less than twice as long as their maximum width, bearing a single large seta near the base, the apex with two large teeth and the inner margin with two or three additional teeth, these teeth surrounding a hol-

lowed-out scoop-like area (teeth may be indistinct due to wear); maxillae with the lacinial area bearing a distinct, angular lobe, but never more than weakly spinulose; galeae slightly to considerably shorter than the maxillary palpi; apical portion of labium on the oral surface with two patches of spinules; spinnerets paired, truncate apically, slightly to considerably exceeding the labial palpi.

Table of Generic and Subgeneric Characters

A. Apex of the maxilla with the surface papillose (fig. 67); maxillary palpi only slightly longer than the galeae; spiracular subatrium elongate, smooth-walled (fig. 66); head strongly roughened on the top and sides and rather strongly setose (fig. 65)
Pison (*argentatum*, [*atrum*])

AA. Apex of maxilla smooth (fig. 42); spiracular subatrium with a series of swellings along its length (figs. 38, 62); head moderately roughened and setose (fig. 36).

B. Posterior end of the body truncate (fig. 39); spinnerets exceeding the labial palpi only slightly (fig. 43)
Trypargilum (*clavatum, johannis, arizonense, spinosum, tridentatum, rubro-cinctum, striatum, politum*)

BB. Posterior end of body somewhat conically produced beyond the anus (fig. 58); spinnerets much exceeding the labial palpi (fig. 60)
Trypoxylon (*s. str.*) (*aldrichi, frigidum, adelphiae, elongatum,* [*figulum*])

Table of Larval Characters of Some Species of Trypargilum [3]

A. Epipharynx with the spinules extending to the apical margin medially (figs. 53, 55); antennal orbits elliptical, pigmented (fig. 54); size large, body length over 20 mm., head width 1.5 mm. or over (Groups *politum* and *punctulatum*).

B. Labrum with about 18-20 setae on the disc (not counting those on the margin) (fig. 53); width of head capsule about 2 mm.
politum Say

BB. Labrum with about 10 setae on the disc (fig. 55); width of head capsule 1.5-1.8 mm. .....*striatum* Provancher

[3] This table is quite tentative, since the available material varies much in quantity and in state of preservation. It is based on mature, non-diapausing specimens. It includes all the Nearctic species except *californicum* Saussure, *collinum* Smith, and *texense* Saussure, larvae of which were not available for study.

AA. Epipharynx with an area medio-apically which is devoid of spinules (fig. 41); body length and head width less than above.

B. Apical margin of labrum more or less trilobed (figs. 41, 49), the median lobe either truncate or concave (Group *spinosum*)

C. Apical margin of labrum concave (figs. 47, 49); western species .....*spinosum* Cameron, *arizonense* Fox

CC. Apical margin of labrum with the median lobe truncate (figs. 41, 44); eastern species *johannis* Richards, *clavatum* Say

BB. Apical margin of labrum evenly concave, without evidence of division into lobes (fig. 50) (Group *nitidum*) *tridentatum* Packard, *rubro-cinctum* Packard

Trypoxylon (Trypargilum) clavatum Say (Plate XIII, figs. 36-43)

Body.—Length 13 mm.; maximum width (abdominal segment 6) 4 mm. (fig. 39). Cylindrical; posterior end blunt, the anus large and ventral in position. Abdominal pleural lobes prominent, set off sharply below from the sterna, above more or less continuous with the swollen posterior annulets; thorax with the pleural lobes somewhat less well defined and placed slightly below the line of the abdominal lobes; apical abdominal segment with a pair of weak lobes dorso-apically. Integument smooth; body with a few small setae, most noticeable on the thoracic dorsum and on the lobes of the anal segment, but also present on each posterior annulet and each pleural lobe. Spiracles weakly pigmented, all about the same size; peritreme well defined; walls of the atrium without noticeable sculpturing; opening into the subatrium simple, unarmed; subatrium long and tapering (fig. 38).

Head.—Considerably broader than high; width 1.16 mm., height .97 mm. (fig. 36). Coronal suture short, weak; parietal bands evident as short, weak lines; epistomal suture strong. Top and sides of the head with numerous small convexities, giving it a roughened appearance. Antennal orbits circular, lightly pigmented, about 50 μ in diameter, with three small sensilla set in the membrane (fig. 37). Head with small punctures, many of which bear setae often as much as 50 μ in length; these are especially numerous laterad of the antennal orbits. Clypeus weakly punctate and bearing several setae.

Mouthparts.—Labrum quadrangular, slightly more than twice as wide as high, measuring .44 mm. wide and .20 mm. high (fig. 41); apical margin with three truncate lobes, the lateral ones extending very slightly beyond the median one; surface with about four setae on the disc on each side of the midline, also with a group on the margin of the median lobe. Epipharynx spinulose except medio-apically, the sensory pores minute. Mandibles .5 mm. long and about .28 mm. in maximum width; upper surface roughened, almost papillose; with two large apical teeth and three smaller teeth along the inner margin, these teeth surrounding a hollowed-out area

(fig. 40). Maxillae smooth apically, devoid of papillae and with only a few short, weak spinules on the lacinial area; inner margin somewhat concave, basally with a large, angular lobe; palpi about 50 μ in length; galeae about 25 μ in length (fig. 42). Labium also rather smooth apically, but with two groups of spines toward the base on the oral surface; palpi about 50 μ long; spinnerets strong, diverging, truncate apically, measuring about 130 μ from the extreme base, about 100 μ from the median point of divergence (fig. 43).

Material.—Eleven specimens, one from Ithaca, N. Y., taken from trap nest, Aug. 16, 1955 (H. E. Evans), one from Derby, N. Y., from trap nest, Aug. 1954 (K. V. Krombein), one from Urbana, Ill., Nov. 18, 1919 (T. H. Frison) [Ill. Nat. Hist. Survey], and eight from Plummers Island, Md., July 11-Sept. 5, 1956, from trap nests (K. V. Krombein).

Trypoxylon (Trypargilum) johannis Richards (Plate XIV, figs. 44-46)

Body.—Length 15 mm.; maximum width 4 mm. Form much as in *clavatum*; posterior annulets prominent, laterally nearly continuous with the pleural lobes; anal segment with the dorso-lateral swellings prominent; anus a transverse slit located ventrally and preapically.

Head.—Width 1.4 mm.; height 1.25 mm. Shape and features much as in *clavatum*, the parietal bands slightly longer, the top and sides of the head slightly more roughened. Antennal orbits nearly circular but with a slight extension mesad and with the sensilla somewhat crowded together in the middle; maximum diameter about 65 μ (fig. 45).

Mouthparts.—Labrum .48 mm. wide and .23 mm. high, very similar to that of *clavatum* but with about ten setae on the disc (fig. 44); epipharynx similar to *clavatum* but apparently with four sensory pores on each side in a small area devoid of spinules. Mandibles .53 mm. long and .32 mm. in maximum width, exactly as in *clavatum*. Maxillae with the lacinial area apparently slightly more strongly spinulose than in *clavatum*; palpi about 55 μ long; galeae about 30 μ long (fig. 46). Labium as in *clavatum*, the two patches of spinules on the oral surface very prominent.

Material.—A single specimen collected from a trap nest, Welaka, Fla., May 11, 1955 (H. E. Evans).

Trypoxylon (Trypargilum) arizonense Fox (Plate XIV, figs. 47-48)

Body.—Length 9 mm.; maximum width 3 mm. Form as described and figured for *clavatum*. Body setae very inconspicuous and few in number.

Head.—Width 1.2 mm.; height 1.12 mm. Shape as in *clavatum*; setae about as in that species; small convexities on the top and sides of the head very noticeable. Coronal suture not visible, the parietal bands barely so. Antennal orbits elliptical, measuring about 50×60 μ (fig. 48).

Mouthparts.—Labrum .48 mm. wide, .20 mm. high on the median line; anterior margin deeply emarginate; surface with five large setae in more or less of a line on each side of the emargination, and with only one other seta plus one or two punctures on the disc (fig. 47). Epipharynx weakly spinulose and virtually devoid of spinules on the sides. Mandibles .5 mm. long, .31 mm. in maximum width, with a single seta near the base; apex as in *clavatum,* but the teeth reduced, probably as a result of wear. Maxillae somewhat pointed apically, the lacinia with rather conspicuous short spinules, much as figured for *johannis* (fig. 46); palpi about 60 μ long, the galeae somewhat smaller. Labium with the palpi about 50 μ long, the spinnerets protruding slightly beyond the palpi; base with two patches of fairly strong spinules, as in other species of the genus.

Material.—Two specimens from Davis, Calif., Sept. 3, 1939 (G. E. Bohart).

Trypoxylon (Trypargilum) spinosum Cameron (Plate XIV, fig. 49)

Body.—Length 13 mm.; maximum width 3.6 mm. Form as described and figured for *clavatum.*

Head.—Width 1.28 mm.; height 1.1 mm. Shape and features as in *clavatum;* parietal bands rather long, weakly pigmented; antennal orbits circular, 50 μ in diameter, the sensilla well separated.

Mouthparts.—Labrum .44 mm. wide, .20 mm. high; apical margin concave and disc with about six setae on each side (fig. 49). Mandibles similar in structure to the preceding several species, but in the available specimens much more blunt, the teeth barely evident, probably as a result of wear. Maxillary palpi rather short and broad, only about 40 μ long; galeae about 30 μ long; lacinial area with the usual angular lobe and only very weakly spinulose. Apex of labium about as described and figured for *clavatum.*

Material.—Three specimens taken from stems at quarantine, Laredo, Texas, Nov. 23, 1942 [U. S. Nat. Mus.].

Trypoxylon (Trypargilum) tridentatum Packard (Plate XIV, figs. 50-52)

Body.—Length 15 mm.; maximum width 4 mm. Form much as in *clavatum*; first thoracic spiracles slightly larger than the others; body setae sparse and inconspicuous.

Head.—Width 1.2 mm.; height 1.02 mm. Features about as in *clavatum*; coronal suture and parietal bands very weak; antennal orbits ovoid, 70 μ in maximum daimeter, the three sensilla in an oblique row (fig. 51).

Mouthparts.—Labrum .5 mm. wide, .2 mm. high on the median line; shape somewhat as in *clavatum,* but the anterior lateral corners more rounded, the anterior margin more concave and without evidence of the

three lobes; disc with six setae on each side in addition to the median marginal group (fig. 50). Epipharynx weakly spinulose, the pores not clearly defined. Mandibles .5 mm. long, .3 mm. in maximum width, features as in *clavatum*. Maxillae somewhat concave apically on the mesal margin, the lacinial area moderately spinulose (fig. 52); palpi about 60 μ in length, galeae about 30 μ in length. Labial palpi 50 μ in length, slightly exceeded by the spinnerets.

Material.—Four specimens, 3 from Kill Devil Hills, Dare Co., N. C., Aug. 15 and Sept. 9-10, 1956, and 1 from 4 mi. W. of Cabin John, Md., Aug. 5, 1955, all collected from trap nests by K. V. Krombein.

Trypoxylon (Trypargilum) rubro-cinctum Packard (Plate XV, fig. 63)

Body.—Length 13 mm.; maximum width 3.5 mm.; setae very inconspicuous; first thoracic spiracles slightly larger than the others.

Head.—Width 1.27 mm.; height 1.1 mm. Shape and features as in *clavatum*. Antennal orbits ovoid, about as in *tridentatum*, measuring 65 × 75 μ.

Mouthparts.—Labrum .44 mm. wide, .19 mm. high on the median line, almost exactly as figured for *tridentatum* (fig. 50). Mandibles .45 mm. long and .26 mm. in maximum width, with five very strong teeth as shown in fig. 63. Maxillae much as in *tridentatum*; palpi about 30 μ long; galeae very small, about 40 μ long. Labial palpi 50 μ in length

Material.—Four specimens, two from Kill Devil Hills, Dare Co., N. C., Aug. 8-Sept. 10, 1956, and two from Plummers Island, Md., July 11-20, 1956, all from trap nests (K. V. Krombein).

Trypoxylon (Trypargilum) striatum Provancher (Plate XIV, fig. 55)

Body.—Length 20 mm.; maximum width 5.5 mm. Form as described for *clavatum*; setae very inconspicuous, distributed as in that species. Spiracles essentially as figured for *clavatum*, but with some indication of the roughening of the walls of the atrium characteristic of *politum*.

Head.—Width 1.5 mm.; height 1.3 mm. Coronal suture weak; parietal bands weak but fairly long. Antennal orbits elliptical, about as figured for *politum* (fig. 54), measuring 60 × 70 μ.

Mouthparts.—Labrum .6 mm. wide, about .3 mm. high; disc with five setae on each side of the median line, and apical margin with a group of setae on the median lobe, which is truncate as in *clavatum*; epipharynx extensively spinulose, the spinules extending practically to the apical margin medially; sensory areas ill-defined, consisting of about six small pores intermingled with the spines plus some very faint larger pores basad of these (fig. 55). Mandibles .56 mm. long, .37 mm. in maximum width, about as figured for *clavatum*. Maxillae rounded apically, very weakly

spinulose on the lacinial area; palpi 70 μ long; galeae 40 μ long. Labial palpi 60 μ long; spinnerets somewhat exceeding the palpi, broad and blunt apically; base of prementum with two patches of setae as in other species of the genus.

Material.—Three specimens from trap nests at Plummers Island, Md., July 11-20, 1956; two specimens from trap nests 4 mi. W. of Cabin John, Md., Aug. 8-9, 1955 (all K. V. Krombein).

Trypoxylon (Trypargilum) politum Say
(Plate XIV, figs. 53-54; Plate XV, fig. 62)

Body.—Length 20 mm.; maximum width 6 mm. Form as in *clavatum*; body setae nearly absent, represented by a few weak ones on the thoracic dorsum. Spiracles (fig. 62) showing numerous swellings on the walls of the atrium which, on the inside, form weak, irregular ridges; subatrium swollen, abruptly tapered.

Head.—Width 2.0 mm.; height 1.75 mm. Shape as in *clavatum*; coronal suture barely evident; parietal bands long but weak; setae relatively short; top and sides of head with many small convexities. Antennal orbits elliptical, darkly pigmented, the sensilla in a more or less straight line; orbit measuring about 70×80 μ (fig. 54).

Mouthparts.—Labrum .83 mm. wide, .37 mm. high on the median line; disc with about nine setae on each side of the median line; apical margin weakly concave, the three lobes weakly defined (fig. 53). Epipharynx strongly spinulose, the spinules extending down to the margin medially. Mandibles similar to other species of the subgenus, but in all the available specimens badly worn, so that the apical teeth are barely evident. Maxillae with the palpi stout, 85 μ in length; galeae more slender, 65 μ in length; lacinial area as in *clavatum*, weakly spinulose. Apex of labium as in *clavatum*, the two patches of setae especially prominent.

Material.—Described from 26 specimens, all taken from mud nests and in a diapausing state, as follows: 14 from Manhattan, Kansas, Feb. 15, 1950 (H. E. Evans); 2 from Urbana, Ill., Mch. 22, 1920 (T. H. Frison) [Ill. Nat. Hist. Survey]; 5 from Selma, Ala., Oct. 25, 1880 [U. S. Nat. Mus.]; and 5 from E. Falls Church, Va., Sept. 14, 1920 [U. S. Nat. Mus.].

Trypoxylon (Trypoxylon) aldrichi Sandhouse (Plate XV, figs. 56-58)

Body.—Length 8 mm.; maximum width 2 mm. (fig. 58). Pleural lobes very prominent, conical, those of the ninth segment especially large, rounded. Anus ventral in position, the anal segment extending well beyond the anus and somewhat conical. Each posterior annulet somewhat swollen on each side of the median line, these swellings indistinctly extending down on the sides to the pleural lobes. Integument smooth; body

with a few weak setae distributed about as in *clavatum*. Spiracles small, circular; structure much as in *clavatum*, but the walls of the atrium with some rather indistinct ridges forming irregular hexagons.

Head.—Width .86 mm.; height .80 mm. Form and features much as illustrated for *clavatum*, but more nearly circular in anterior view and the antennal orbits relatively a little larger and lower. Coronal suture very weak; parietal bands not present. Setae distributed about as in *clavatum* and the top and sides of the head similarly roughened. Antennal orbits elliptical, about 40×50 μ in size, the three sensilla close together in the middle (fig. 57).

Mouthparts.—Labrum .31 mm. wide, about .13 mm. high medially (fig. 56); antero-lateral corners slightly produced, anterior margin weakly emarginate; disc with eight setae and the anterior margin with about six setae near the midline. Epipharynx with the spinules small, rather far apart except on the anterior lateral corners, where they are crowded. Mandibles .31 mm. long, .2 mm. in maximum width, exactly as in *clavatum* except that the roughening of the surface is less evident. Maxillae rounded apically, the lacinial area with a distinct but weakly spinulose angular lobe; palpi stout, 40 μ in length; galeae more slender, 22 μ in length. Apex of labium very much as figured for *clavatum*; palpi only about 30 μ in length; spinnerets truncate apically, measuring about 80 μ from base to apex, surpassing the palpi by about 40 μ; oral surface with the usual two patches of spinules, the spinules short and rather sparse.

Material.—One specimen from an elderberry stem, Logan, Utah, June 2, 1954 (G. E. Bohart).

Trypoxylon (Trypoxylon) frigidum Smith (Plate XV, figs. 59-60)

Body.—Length 7.5 mm.; maximum width 1.6 mm. Features as described and figured for *aldrichi*; tenth abdominal segment well produced beyond the anus, but somewhat more rounded than in *aldrichi*; pleural lobes prominent, especially those on the thorax and on abdominal segment nine.

Head.—Width .75 mm.; height .73 mm.; in anterior view nearly circular. Features as in *aldrichi*, including size and shape of the antennal orbits.

Mouthparts.—Labrum .27 mm. wide; features as in *aldrichi* but with ten setae on the disc (fig. 59); epipharynx as in *aldrichi*, a few minute sensory pores evident on each side. Mandibles .29 mm. long and .17 mm. in maximum width, of the usual form in the genus but with scarcely any roughening of the upper surface; apical teeth sharp and much as illustrated for *rubro-cinctum* (fig. 63). Maxillae as in *aldrichi*; palpi 40 μ long; galeae slender, 30 μ long. Labial palpi 30 μ long, the spinnerets about 80 μ long and much exceeding the palpi (fig. 60).

Material.—One specimen from Derby, N. Y., June 28, 1956 (L. H. Krombein).

Trypoxylon (Trypoxylon) adelphiae Sandhouse (Plate XV, fig. 61)

Body.—Length 8 mm.; maximum width 1.7 mm. Features as described and figured for *aldrichi*; anal segment somewhat conical as in that species.

Head.—Width .83 mm.; height .75 mm. Form and features as in *aldrichi*, antennal orbits also the same size and shape as in that species.

Mouthparts.—Labrum .3 mm. wide; anterior margin somewhat more narrowly emarginate than in the preceding two species; disc with about twelve setae plus a few more on the margin medially (fig. 61). Epipharynx somewhat more heavily spinulose than in *aldrichi*, and with four very small sensory pores on each side. Mandibles .29 mm. long, .18 mm. wide at the base, much as in the preceding two species but with the roughening of the upper surface much stronger, much as in the species of *Trypargilum*. Features of the maxillae and labium as described for *aldrichi*; maxillary palpi 45 μ long; galeae 30 μ long; labial palpi 40 μ long; spinnerets extending well beyond the labial palpi.

Material.—One specimen from Plummers Island, Md., July 20, 1956 (K. V. Krombein).

Trypoxylon (Trypoxylon) elongatum Ashmead

Williams (1919, Hawaiian Sugar Planters' Assoc. Exp. Sta., Ent. Ser., Bull. no. 14, pp. 143-145) has briefly described the larva of this Philippine species. The full-grown larva is said to be 18.5 mm. long, with well-developed dorsal and lateral protuberances; "the tip of the body is obliquely subtruncate and the thorax is armed with a few bristles." His figure shows a body form identical to that of the North American species of this subgenus. Williams made a balsam mount of the head capsule, which I have examined. The width of the head capsule is 1.35 mm., the height slightly less than this; the coronal suture and parietal bands are not visible; the antennal orbits are obliquely elliptical, about 55 μ in maximum diameter. The mandibles are of the usual form in the genus, but without any evident roughening on the upper surface. The spinnerets appear to be about twice the length of the labial palpi.

Material.—A single head capsule mounted in balsam, from Los Baños, Philippines, 1917 (F. X. Williams).

Trypoxylon (Trypoxylon) figulum (Linnaeus)

The larva of this Holarctic species has been described very briefly by Soika (1934, Ann. Soc. Ent. France, 103: 342-343, pl.

III, fig. II). The resemblance to the preceding four species is strong. The antennal orbits are round, the anterior margin of the labrum gently concave. The epipharynx is sparsely spinulose but the spinules apparently no more dense antero-laterally than elsewhere. The features of the mandibles, maxilla, and labium, so far as described, agree well with the other species of this subgenus.

Pison argentatum Shuckard (Plate XVI, figs. 65-68)

Body (diapausing larva).—Length 8 mm.; maximum width 2.6 mm. Form very similar to that of the species of *Trypargilum*; posterior end truncate, the anus located ventrally on the last segment; pleural lobes strong, the posterior annulets also swollen, particularly just to each side of the median dorsal line. A very few setae are present on the thoracic dorsum. Spiracles with the walls of the atrium completely smooth; opening between atrium and subatrium with some weak folds or spines; subatrium slender, without swellings along its length (fig. 66).

Head.—Width 1.12 mm.; height .96 mm.; in anterior view subcircular, a little flattened on top (fig. 65). Top and sides roughened with many small convexities. Coronal suture and parietal bands not evident. Setae numerous and fairly strong. Antennal orbits transversely ovoid, 70 μ in greatest diameter.

Mouthparts.—Labrum .38 mm. wide, .19 mm. high on the median line; apical margin feebly emarginate, with a series of minute sensory cones and a few setae; disc with about 12 setae (fig. 68). Epipharynx with five small sensory cones on each side; spinules sparse, somewhat more crowded toward the lateral margins. Mandibles with a single seta near the base; apex rather blunt, probably due to wear, in general about as in *Trypoxylon;* length .42 mm., maximum width .27 mm. Maxillae rounded apically, the surface papillose; lacinial area with an angular, somewhat spinulose lobe, as in *Trypoxylon*; palpi stout, about 60 μ in length; galeae much more slender, about 50 μ in length (fig. 67). Apex of labium much as illustrated for *Trypoxylon clavatum* and with the same two patches of spinules; palpi about 50 μ in length; spinnerets blunt apically, slightly surpassing the palpi.

Material.—Six specimens from cocoons collected from a clay bank on Mt. Moto, Ishigaki Island, So. Ryukyus, Dec. 24, 1952 (G. E. Bohart).

Pison sp. (Plate XV, fig. 64)

Body.—Length 9 mm.; maximum width 2.5 mm. Pleural lobes distinct, those on the prothorax and mesothorax strongly protuberant, conical; each posterior annulet strongly elevated, except with a median dorsal depres-

sion. Posterior end bluntly rounded, the anus a transverse slit located ventrally. Integument smooth; thoracic dorsum with a very few small setae. Spiracles as described for *argentatum*.

Head.—Width 1.25 mm.; height 1.0 mm.; shape and features as described for *argentatum*. Antennal orbits ovoid, 60 μ in greatest diameter.

Mouthparts.—Labrum .43 mm. wide, .2 mm. high on the median line; apparently more strongly emarginate than in *argentatum* and with more setae in the emargination (fig. 64). Mandibles .47 mm. long, .29 mm. in maximum width, similar to *argentatum*. Maxillary palpi stout, 60 μ long; galeae more slender, about 55 μ long. Labium as in *argentatum*, the palpi about 55 μ long.

Material.—Five specimens from Milne Bay, New Guinea, March 1944 (K. V. Krombein). It is possible that these specimens are also *argentatum*; certainly the differences are slight.

Pison atrum (Spinola)

Micheli (1933, Mem. Soc. Ent. Italiana, 12: 8-10) has presented a detailed description of the diapausing larva of this Palaearctic species. The resemblance to *argentatum* is very close. The head is somewhat flattened on top, the coronal suture and parietal bands absent, the antennal orbits circular. The labrum and epipharynx are very much the same as in *argentatum*. The mandibles are of typical *Trypoxylon*-type, with four evident teeth and some roughening of the upper surface. Micheli does not indicate that the apex of the maxilla is papillose, as it is in the above two species, and he shows the galeae as being considerably shorter than the maxillary palpi. The lacinial lobe is shaped as in *argentatum* and similarly spinulose.

Subfamily Crabroninae

This section is of a very preliminary nature. Of the 15 genera of Crabroninae listed in the Synoptic Catalog of Hymenoptera of America North of Mexico (1951, U. S. Dept. Agri., Monogr. no. 2) I have seen larvae of only six. The larvae of three other genera have been described by European workers, making a total of nine out of 15 genera in which the larvae are to some degree known. There are many exotic genera, and also several subgenera of the known Nearctic genera, in which the larvae remain undescribed. Fortunately, the known larvae are sufficiently similar to make possible a subfamilial diagnosis which is

probably fairly valid. In general, the larvae of Crabroninae resemble those of the Trypoxyloninae very closely, the most notable difference being the complete absence of an angular lacinial lobe. The arrangement of the genera in the text follows that in the Synoptic Catalog.

Characters of the subfamily.—Body rather stout, somewhat grub-like; pleural lobes strongly developed; anus situated ventrally and preapically, the tenth segment either truncate or slightly produced beyond the anus; integument sometimes completely smooth, but more often with very small spinules which are irregularly distributed and generally separated from one another by more than their own length; body setae present on parts of the dorsum and pleura, but always very small and sparse; spiracles with the atrium smooth-walled or lined with a network of fine ridges; opening into the subatrium simple, unarmed; subatrium elongate. Head wider than high; parietal bands weak or absent; antennal papilla absent, the three sensilla arising from the membrane of the orbit, which may be slightly elevated; head always with numerous fairly long setae. Labrum of simple structure, the disc with numerous strong setae, the apical margin fringed with small spines, but without noticeable sensory cones or stout setae set in the margin; epipharynx strongly spinulose, at least in part, the sensory pores or cones set in smooth areas well back from the anterior margin; mandibles of variable structure, usually about twice as long as their maximum width, with one or rarely two stout setae on the side near the base; maxillae simple, the lacinia without a lobe, but with dense, rather long spinules; maxillary palpi always longer and stouter than the galeae; labium with at least part of the oral surface clothed with spinules; spinnerets paired, long and slender, always exceeding the labial palpi and sometimes up to as much as three times the length of the palpi; spinnerets usually truncate apically.

Table of Tribal and Generic Characters [4]

A. Epipharynx with the spinules extending to the apical margin medially, or nearly so (figs. 69, 79); lacinial area spinulose, without papillae intermingled with the spinules (figs. 83, 92)
CRABRONINI

B. Mandibles simple, with only the apical tooth; labrum rather deeply emarginate .....*Tracheliodes* [*5-notatus*]

BB. Mandibles with from three to five teeth.

C. Mandibles with three or four teeth (figs. 72, 100), in lateral view without a tooth visible part way out on the hind margin (figs. 96, 97, 101).

D. Mandibles with three teeth, the penultimate tooth of the other genera apparently absent; galeae very small .....*Lindenius* [*pygmaeus*]

DD. Mandibles with four teeth (figs. 72, 100).

E. Integument smooth, entirely without spinules; teeth of mandibles in nearly the same plane, in lateral view the penultimate tooth only slightly evident (fig. 101)
Euplilis (*arapaho, pedicellatus,* [*coarctatus, clavipes*])

EE. Integument with small spinules evident under high magnification (at least on some parts of the body); apex of mandibles, in lateral view, usually more evidently bifid (figs. 96, 97).

F. Lacinial area with short spinules; oral surface of labium wholly covered with short spinules .....*Entomognathus* [*brevis*]

FF. Lacinial area with longer and more flexible spinules (fig. 73); labium with longer spinules in a more circumscribed area.
Crabro (*advenus*), *Crossocerus* (*ambiguus, fergusoni,* [*cinxius, capitosus, pubescens, walkeri, varus, quadrimaculatus, podagricus*])

CC. Mandibles with five teeth, the fifth tooth located on the ventral side and not readily visible from above (figs. 82, 87, 88), in lateral view the fifth tooth visible on the hind margin part way out (figs. 80, 89).

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[4] This table will doubtless require much modification when the larvae of more genera are known (at present 9 out of 15, with 3 of the 9 known only from descriptions by European writers). I have been unable to separate the larvae of *Crabro* and *Crossocerus* on the basis of available material. The characters given for the separation of the tribes Crabronini and Oxybelini are of a rather minor nature and may not hold for all genera of both tribes.

D. Apex of mandibles not hollowed out ventrally, the base of the mandibles with two setae (fig. 82); labium with two patches of very long spines (fig. 84) .....*Anacrabro* (*ocellatus*)

DD. Apex of mandibles hollowed out on the ventral side, the base with only one seta (figs. 87, 88); labium with much shorter spinules (fig. 93).
Ectemnius (*stirpicolus, atriceps, tumidoventris,* [*zonatus, cavifrons, guttatus*])

AA. Epipharynx with the spinules mostly on the base and sides, leaving a large area medio-apically bare or bearing papillae (figs. 105, 111); lacinial area both papillose and spinulose, some of the papillae commonly intermingled with the spinules (fig. 113); mandibles with five teeth (fig. 114)
OXYBELINI, *Oxybelus* (*bipunctatus, quadrinotatus,* [*melacholicus, argentatus*])

Tribe Crabronini

Anacrabro ocellatus Packard (Plate XVII, figs. 75-84)

Body.—Length 7.5 mm.; maximum width (abdominal segment 5) 2.3 mm. (fig. 78). Grub-like, somewhat curved; pleural lobes prominent, rounded, those on the thorax somewhat lower than those on the abdomen; anus situated ventrally on the tenth abdominal segment, which is blunt. Integument smooth except for irregularly distributed short spinules, visible only under high magnification; these spinules are generally separated from each other by more than their length (fig. 81). Body also with a few small setae dorsally and on the pleural lobes. Spiracles small, lightly pigmented; atrium with a meshwork of weak ridges lining the walls; opening into the subatrium unarmed; subatrium elongate (fig. 76).

Head.—Width 1.15 mm.; height .96 mm. (fig. 75). Coronal suture short, unpigmented; parietal bands absent; epistomal suture indistinct. Top and sides with numerous small convexities, giving the head a roughened appearance. Antennal orbits circular, 45 μ in diameter (fig. 77). Head with numerous strong setae, many of them as much as 300 μ in length, especially abundant on the lower sides. Clypeus with several strong setae in a row.

Mouthparts.—Labrum .43 mm. wide, its apical margin rounded, with a very weak median emargination; margin spinose; surface with numerous large setae (fig. 79). Epipharynx spinulose, the spinules grading into papillae latero-basally, with about four sensory cones in an unpigmented area on each side well back from the margin. Mandibles .52 mm. long, .28 mm. wide near the base; base with two strong setae laterally; inner margin with four teeth in about the same plane, plus a fifth tooth which is in a different plane and beneath the others (fig. 82); in lateral view this fifth tooth is prominent on the posterior margin of the mandible (fig. 80). Maxillae with the palpi about 80 μ long, the galeae much smaller, about

40 μ long; lacinial area densely clothed with long, flexible setiform spines (fig. 83). Labium with the palpi 70 μ long, only about 50 μ actually extending beyond the apex of the labium; spinnerets elongate, truncate apically, extending beyond the apex of the labium for about 100 μ; oral surface of labium with two patches of very long, flexible spines (fig. 84).

Material.—Three specimens from Ithaca, N. Y., July 1953 (M. A. Evans).

Entomognathus brevis (Van der Linden)

Grandi (1927, Redia, 16: 74-77) has described the larva of this Palaearctic species in some detail. The body is grub-like, shaped much as in *Anacrabro,* but the position of the anus is not indicated. The integument is sparsely clothed with short spines and bears a few setae, as in *Anacrabro.* The head shape is about as in that genus, but the setae appear to be somewhat shorter and more regularly arranged on the sides of the head. The labrum does not differ noticeably from that of *Anacrabro.* The mandibles have four teeth, subequal in size and all in about the same plane (about as figured for *Euplilis,* fig. 100). Both the lacinial area and the oral surface of the labium are extensively covered with close-set, short spinules. The spinnerets extend beyond the margin of the labium to about twice the length of the palpi.

Lindenius pygmaeus (Rossi)

Grandi has also described the larva of this Palaearctic species (1928, Boll. Lab. Ent. Bologna, 1: 310-312). The body form is much as in *Anacrabro,* but a bit more slender; the tenth abdominal segment is rounded, lobe-like, the position of the anus not indicated. The features of the head and of the labrum are very much as in *Anacrabro.* The mandibles have but a single seta near the base, and the inner margin has but three teeth, the penultimate tooth of the other genera apparently being absent. The maxilla is papillose apically and the lacinial area bears long, flexible spines; the palpi are very large and the galeae unusually small. The spinnerets are about twice the length of the labial palpi.

Tracheliodes 5-notatus (Jurine)

The larva of this Palaearctic species has also been described by Grandi (1927, Boll. Lab. Ent. Bologna, 1: 25-26). The body

form is similar to that of *Anacrabro*, but more slender; the tenth abdominal segment is somewhat pointed, the anus distinctly preapical in position. The features of the head are much as described for *Anacrabro*; the labrum is setose as in that genus, but the apical margin is more deeply emarginate and apparently not fringed with spines. The mandibles are said to be simple and edentate, tapering gradually to an acute apex. The maxillary galeae are much shorter than the palpi and the lacinial area is spinulose. The labium possesses rather long palpi, and the spinnerets exceed the palpi only slightly; the oral surface has two patches of spinules which are very much shorter than in *Anacrabro*.

Crabro advenus Smith (Plate XIX, figs. 95-96)

Body.—The body of the single available specimen is not well preserved. The integument appears to be covered with small, widely separated spinules as in *Anacrabro*.

Head.—Width 1.15 mm.; height .95 mm. Coronal suture indistinct, but the parietal bands apparently present as weak lines of slightly darker pigmentation. Top and sides of head capsule only very weakly roughened; head setae very small, the longest ones only about 25 μ in length. Antennal orbits circular, about 45 μ in diameter, the three sensilla located on top of a somewhat dome-like elevation.

Mouthparts.—Labrum .35 mm. wide, the apical margin rounded and with only a very weak median emargination; apical margin fringed with long setae, especially laterally; disc with numerous strong setae (fig. 95). Epipharynx with abundant strong spinules medially, grading into smaller spinules and papillae laterally; sensory areas consisting of five very small cones in a group and some weaker pores basad of these. Mandibles much as figured for *Euplilis arapaho* (fig. 100), with four teeth which are in nearly the same plane and nearly equal in size; in lateral view (fig. 96) only the penultimate tooth is prominent, the apex thus somewhat bifid; base with one seta. Maxillae much as in *Anacrabro*; lacinial area with dense, long, flexible spinules; palpi conical, 70 μ in length; galeae small and slender, 35 μ in length. Apex of labium with dense, fairly long spines on the upper surface (shorter than in *Anacrabro*); palpi 60 μ long; spinnerets much exceeding the palpi.

Material.—One specimen from Snow Hill, Md., 29 May 1952 (W. H. Anderson) [U. S. Nat. Mus.].

Euplilis arapaho Pate (Plate XIX, figs. 99-103)

Body.—Length about 4 mm. The body of the single available specimen is not well preserved, but it appears to resemble closely that of *Anacrabro*

ocellatus except that it is more slender. The pleural lobes are very strong, and each posterior annulet bears a strong transverse elevation which is interrupted medially. The posterior end of the body is rounded and the anus situated preapically. The integument is completely smooth and without any spinules whatsoever; a few minute setae are present on the thoracic dorsum. The spiracles are simple, the atrium without sculpturing, the subatrium somewhat more elongate than in *Anacrabro*.

Head.—Width .58 mm.; height .54 mm. Shape much as in *Anacrabro*; parietal bands absent; coronal suture weak but fairly long. Top and sides of head rather strongly roughened by many small convexities. Setae confined largely to the periphery of the head, as seen in anterior view, considerably fewer in number than in *Anacrabro*, the longest ones about 30 μ in length. Antennal orbits ovoid, about 40 μ in greatest diameter, the three sensilla located on a dome-like elevation of the membrane of the orbit. Epistomal suture distinct; clypeus with a very few setae.

Mouthparts.—Labrum .2 mm. wide, .09 mm. high on the median line; apex subtruncate; disc with a few setae and apical margin strongly spinose; epipharynx strongly spinulose, the sensory areas consisting of a small group of sensilla above which are several large pores (fig. 99). Mandibles .27 mm. long, .13 mm. in maximum width; base with a single seta; inner margin with four teeth, all about equally developed, but the penultimate somewhat the most prominent (figs. 100, 101). Maxillae with the palpi about 40 μ in length, the galeae about 30 μ in length; lacinial area with dense long spinules which are directed outward (fig. 102). Apex of labium with numerous strong spines on the oral surface; palpi about 35 μ in length; spinnerets measuring about 50 μ from base to apex, only slightly exceeding the palpi (fig. 103).

Material.—One specimen from *Sambucus* stem, Logan, Utah, 1948 (G. E. Bohart).

Euplilis pedicellatus (Packard) (Plate XIX, fig. 104)

Packard (1896, Jour. N. Y. Ent. Soc., 4: 161-163) presented a brief description and sketch of the larva of this species. According to him, the body terminates in " a small knob-like portion " and the body is sparsely clothed with rather long setae. The only material of this species available to me is a single cast skin taken from a cocoon.

Body.—With a few small, widely scattered setae. Integument smooth, without any evidence of spinules. Spiracles as described for *arapaho*.

Head.—Essentially as described for *arapaho*. Antennal orbits circular, 40 μ in diameter.

Mouthparts.—Labrum .18 mm. wide, .09 mm. high, much as in *arapaho* but with the setae more spread out over the disc; epipharynx with long

spinules more confined to the apical margin than in *arapaho* (fig. 104). Mandibles with a single seta basally, with four strong teeth along the inner margin, the antepenultimate the weakest. Maxillae about as figured for *arapaho*; palpi and galeae about the same length. Labium with the palpi about 30 μ long, the spinnerets much exceeding the palpi, about 65 μ long.

Material.—A single cast larval skin from a cocoon in a rose stem, sent to the author from Dayton, Ohio, May 5, 1956.

Euplilis coarctatus (Scopoli)

The larva of this Palaearctic species has been described by Micheli (1929, Boll. Soc. Ent. Italiana, 61: 34-35). Nothing is said about the nature of the integument or the body setae. The labrum bears a somewhat larger number of setae than in the known American species, but otherwise the labrum and epipharynx are very similar. The mandibles have four subequal teeth along the inner margin. The maxillae and labium are much as in *arapaho* except that the spinnerets protrude far beyond the labial palpi.

Euplilis clavipes (Linnaeus)

Maréchal (1929, Ann. Soc. Ent. France, 98: 115-116) has described the larva of this species. The body form is much as figured for *Crossocerus ambiguus* (fig. 71); setae are said to be present on the body, also a few on the head capsule. The head is subcircular in anterior view, the labrum shaped much as in *arapaho*. The mandibles have four sharp teeth along the inner margin. The maxillary palpi considerably exceed the galeae and the spinnerets much exceed the labial palpi.

Crossocerus (Coelocrabro) ambiguus (Dahlbom)

(Plate XVI, figs. 69-74)

Body.—Length 6 mm.; maximum width 2 mm. (fig. 71). Form similar to *Anacrabro ocellatus*, but more slender; pleural lobes very prominent; anal segment roundly protuberant, the anus ventral and preapical. Integument clothed sparsely and irregularly with minute spinules, much as in *Anacrabro*. Body without setae except for a few inconspicuous ones on the thoracic dorsum. Spiracles with the atria lined with a few weak ridges which tend to form large hexagons.

Head.—Width .7 mm.; height .66 mm.; subcircular in anterior view; coronal suture weak; parietal bands absent; epistomal suture distinct. Top and sides of the head weakly roughened, provided with numerous

setae, the longest setae about 40 μ in length. Antennal orbits transversely ovoid, 50 μ in greatest diameter, the membrane of each orbit elevated and bearing three sensilla (fig. 74).

Mouthparts.—Labrum .21 mm. wide, .10 mm. high; disc with numerous setae and apical margin bristly; epipharynx strongly spinulose, the sensory areas each consisting of several small sensilla plus a few pores basad of these (fig. 69). Mandibles .32 mm. long and .17 mm. wide at the base, with a single seta near the base; inner margin somewhat crenulate, with four rather poorly defined teeth (fig. 72). Maxillae rounded apically, the surface weakly papillose, the lacinial area with dense, erect spinules; palpi about 55 μ long, galeae about 25 μ long (fig. 73). Labium strongly spinulose on the oral surface; palpi about 35 μ long; spinnerets about 70 μ long (fig. 70).

Material.—Four specimens from Ithaca, N. Y., August 27, 1954 (C. S. Lin).

Crossocerus (Coelocrabro) fergusoni Pate (Plate XIX, figs. 97-98)

Body.—Length 6 mm.; maximum width 2 mm. Form similar to *ambiguus*; posterior annulets very prominent, especially anteriorly; pleural lobes also very prominent, especially on the thorax. Integument sparsely and irregularly clothed with minute spinules. Spiracles with the atrium lined with irregular hexagons, the subatrium very long, slender, and smooth (fig. 98).

Head.—Width .86 mm.; height .76 mm. Parietal bands apparently represented by weakly pigmented streaks. Antennal orbits shaped as in *ambiguus*, 50 μ in maximum diameter. Head with relatively few setae, the longest setae only about 25 μ in length, the setae situated mostly on the sides of the head.

Mouthparts.—Labrum .28 mm. wide, .14 mm. high on the median line; shaped as in *ambiguus* and very similar to that species; epipharynx also much as in *ambiguus* but somewhat more coarsely spinulose medially and anteriorly. Mandibles with a single seta near the base; inner margin with four very strong, subequal teeth, the penultimate tooth very strong and projecting in a slightly different plane from the others, such that in lateral view the mandibles appear bifid at the apex (fig. 97). Maxillae as figured for *ambiguus* but with the galeae relatively shorter, only about 15 μ long, scarcely longer than thick. Labium with the palpi about 40 μ in length, the spinnerets about 90 μ in length.

Material.—Three specimens from cocoons in elderberry stem, Logan, Utah, June 1948 (G. E. Bohart).

Crossocerus (Coelocrabro) cinxius (Dahlbom)
Crossocerus (Coelocrabro) capitosus (Shuckard)
Crossocerus (Coelocrabro) pubescens (Shuckard)
Crossocerus (Coelocrabro) walkeri (Shuckard)

The larvae of these four species of the subgenus *Coelocrabro* have been described by various European workers. All seem to resemble closely the two American species described above. In all of them the mandibles have four strong teeth, with the apical two juxtaposed so that the apex is strongly bifid in lateral view (as in *fergusoni*). The parietal bands appear to be distinct in *pubescens,* absent in the others. In all of them the spinnerets much exceed the labial palpi. References to the descriptions are as follows: *cinxius,* Micheli, 1930, Mem. Soc. Ent. Italiana, 9: 55-56; *capitosus,* Maréchal, 1927, Ann. Soc. Ent. France, 96: 105-106; *pubescens,* Baudot, 1934, Ann. Soc. Ent. France, 103: 383; *walkeri,* Baudot, 1929, Bull. Zool. Soc. France, 54: 498-500.

Crossocerus (Ablepharipus) podagricus (Van der Linden)

Goidanich (1928, Boll. Lab. Ent. Bologna, 1: 103-106) has provided a detailed and well-illustrated description of this species. The head is sparsely setose; the labrum is truncate apically and otherwise much as in *ambiguus.* The mandibles have four strong teeth and a single seta near the base. The spinnerets taper strongly from a rather broad base and are only about twice the length of the labial palpi. All in all, the resemblance to the two American species described above is very great, and there are no obvious differences which might be considered of subgeneric value.

Crossocerus (Stenocrabro) varus Lepeletier

Maneval (1939, Ann. Soc. Ent. France, 108: 82-83) has supplied a short description of this species. The mandibles are rather weakly quadridentate and, in lateral view, weakly bifid apically, much more as in *ambiguus* than as in *fergusoni* and the five Palaearctic species discussed above. The spinnerets are exceedingly long and slender. The galeae also agree with *ambiguus* in being rather slender and elongate. The head has abundant setae.

Crossocerus (Hoplocrabro) quadrimaculatus (Fabricius)

Maneval (1939, op. cit., pp. 85-86) has also described the larva of this species. The mandibles have three strong teeth and a weak fourth tooth basad of these; the apical two teeth are juxtaposed so that the apex is bifid in lateral view. The head

has many small setae and the labrum an unusual number of setae. The galeae are very slender and fairly long, the spinnerets very long and spiniform.

Ectemnius (Hypocrabro) stirpicolus (Packard)
(Plate XVIII, figs. 85-90)

Body.—Length 7 mm.; width 2.2 mm. Very much as figured for *Crossocerus ambiguus*; last abdominal segment rounded, extending well beyond the anus. Integument smooth, but with a few widely scattered minute spinules visible under high power on certain parts of the body; body setae very sparse, short, and inconspicuous. Spiracles (fig. 86) much as in *Crossocerus,* but the subatrium with a bulbous expansion close beneath the atrium.

Head.—Width .8 mm.; height .73 mm. (fig. 85). Orbits lightly pigmented; anterior tentorial arms and pleurostomal and hypostomal thickenings heavily pigmented; mandibles brown; palpi and galeae light brown; posterior aspect of head with paired pigment spots beneath the foramen and the maxilla with a pigmented bar as illustrated. Coronal suture very weak; parietal bands represented by weak pigmented lines. Setae sparse and rather short, the longest ones about 30 μ long. Antennal orbits unusually small, transversely ovoid but approaching circular, about 40 μ in diameter.

Mouthparts.—Labrum .24 mm. wide, .12 mm. high; apical margin weakly rounded, bristly; disc with a few setae (fig. 90). Epipharynx strongly spinulose, especially medially and anteriorly. Mandibles with five teeth, one of the teeth ventral in position and not visible from above; apical two teeth juxtaposed in such a way that in lateral view the apex is strongly bifid; ventral surface hollowed out apically, much as in *Trypoxylon;* base with a single seta; length .34 mm., maximum width .18 mm. (figs. 87-89). Maxillae much as figured for *Crossocerus,* rounded and smooth apically, the lacinial area with dense, rather long, flexible setae which are directed outward; palpi 60 μ long, galeae slender, 40 μ long. Labial palpi 30 μ long, considerably exceeded by the spinnerets; oral surface of labium with a large patch of rather long, flexible setae.

Material.—Two whole specimens plus several cast skins, all taken from cocoons in rose stems sent to the writer from Dayton, Ohio, May 1956.

Ectemnius (Ectemnius) atriceps (Cresson) (Plate XVIII, figs. 91–94)

Body.—Not well preserved in the available material. Integument with very minute, unevenly distributed spinules and with a few small setae in certain areas. Spiracles as figured for *stirpicolus.*

Head.—Width .96 mm.; height .83 mm. Features much as in *stirpicolus,* but the parietal bands considerably stronger, about .25 mm. in length.

Antennal orbits small, ovoid, 50 μ in greatest diameter, with a central, circular pigmented area bearing only two sensilla (at least on both sides of the single available specimen) (fig. 94). Longest setae of the head about 30 μ in length.

Mouthparts.—Labrum .28 mm. wide, .14 mm. high; apical margin bristly, very weakly emarginate medially, the disc with about 10 setae on each side (fig. 91). Epipharynx strongly spinulose medially and apically, papillose toward the base. Mandibles .42 mm. long, .21 mm. in maximum width, exactly as figured for *stirpicolus*. Maxillae rounded apically, the lacinial area with rather long, slender spines; palpi 70 μ in length; galeae 40 μ in length (fig. 92). Labium with moderately long spines on the oral surface; palpi 40 μ long; spinnerets prominent, about 80 μ long (fig. 93).

Material.—A single specimen from a cocoon in a *Sambucus* stem, Logan, Utah, April 1948 (G. E. Bohart).

Ectemnius (Ectemnius) guttatus (Van der Linden)

The larva of this species has been described briefly and figured rather crudely by Minkiewicz (1932, Polskie Pismo Ent., 10: 214-215, under the name *spinicollis*). The apical two teeth of the mandibles appear to be juxtaposed in the manner of *stirpicolus* and *atriceps,* but the mandibles are otherwise not described adequately. The apex of the maxilla and of the labium agree fairly closely with the American species. The antennal orbits are not described or figured.

Ectemnius (Oreocrabro) tumidoventris (Perkins)

Williams (1927, Proc. Haw. Ent. Soc., 6: 448) has sketched the larva of this Hawaiian species, and the slides which he made of the head capsule have been loaned to me by the Hawaiian Sugar Planters' Experiment Station.

Body.—As figured by Williams, somewhat fusiform and with very prominent posterior annulets and pleural lobes; anal segment protruding as a rounded lobe; thorax with a few weak setae.

Head.—Width 1 mm.; height .95 mm. Coronal suture and parietal bands not visible in the available preparations; setae small, few in number, about as in *stirpicolus*. Antennal orbits small, circular, about 40 μ in diameter.

Mouthparts.—Labrum .32 mm. wide, the apical margin subtruncate; disc with a large number of setae (about as in *atriceps*); margin strongly spinose. Mandibles with five teeth and exactly as figured for *stirpicolus*. Maxillae smooth and rounded apically; palpi 80 μ long; galeae 50 μ long;

lacinial area with dense, flexible spines. Labial palpi 50 μ long; spinnerets 70 μ long, exceeding the palpi only slightly.

Material.—Described from two head capsules mounted in balsam by F. X. Williams, specimens from Kilauea, Hawaii, Nov. 1919.

Ectemnius (Clytochrysus) zonatus (Panzer)

Maneval (1937, Rev. Franc. Ent., 4: 167-169) has provided a rather full description of this species. The head is subcircular in anterior view, slightly wider than high, with the parietal bands absent and the antennal orbits unusually small, each with three sensilla. The mandibles are bifid apically and possess a single additional rounded tooth on the inner margin. The spinnerets and the labial palpi are both unusually long and slender. The mandibles appear to differ considerably not only from those of *stirpicolus, atriceps,* and *tumidoventris,* but also from those of another species of *Clytochrysus, cavifrons,* as described by Leclercq (see below). It is possible that the mandibles of Maneval's specimens were badly worn.

Ectemnius (Clytochrysus) cavifrons (Thomson)

Leclercq (1954, Monographie systematique . . . des Hyménoptères Crabroniens, p. 25) presents an excellent figure of the head capsule of this species. The resemblance to the American species *stirpicolus* and *atriceps* is very striking. The parietal bands are fairly strong and the antennal orbits small. The mandibles are exactly as figured for *stirpicolus.* The labrum, maxillae, and labium are not sketched in detail, but as far as can be seen they do not differ notably from the American species.

Tribe Oxybelini

Oxybelus bipunctatus Olivier (Plate XX, figs. 107-115)

Body.—Length 7.5 mm.; maximum width 2.5 mm.; fusiform, slightly thicker posteriorly; pleural lobes rounded, very prominent on the thorax but less so on the abdomen; anus ventral and preapical, the apex of the abdomen forming a distinct rounded lobe (fig. 109). Integument smooth, sparsely clothed with minute spinules which vary in size and shape and are rather irregularly distributed (fig. 110). Body with a few small setae dorsally. Spiracles with the atrium rather broad and shallow, lined with a few weak ridges; subatrium elongate (fig. 108).

Head.—Width .83 mm.; height .7 mm.; subcircular in anterior view (fig. 107). Coronal suture and parietal bands not visible. Epicranium very weakly roughened by small convexities; setae sparse but fairly long, the longest measuring about 50 μ. Antennal orbits small, circular, 30 μ in diameter.

Mouthparts.—Labrum .32 mm. wide, about .14 mm. high on the median line; apical margin weakly emarginate medially; surface with a few large setae (fig. 111). Epipharynx mostly bare medio-apically, but with dense spines basally and laterally; sensory areas unpigmented, each with about six small pores. Mandibles .40 mm. long, .19 mm. wide at the base; base with a single seta; apex with five teeth surrounding a ventral excavation, much as in *Ectemnius* (fig. 114); in lateral view, apex bifid and two other teeth visible below the apex (fig. 115). Maxillae rounded apically, densely papillose, the lacinial area with strong spinules among the papillae; palpi 50 μ long; galeae 25 μ long, ending in two distinct sensilla (fig. 113). Labium with the palpi 45 μ long, one of the apical sensilla unusually large; spinnerets long and pointed, measuring 80 μ from the base; oral surface papillose and with a group of very long, slender spines on each side below the palpus (fig. 112).

Material.—Fifteen specimens from Ithaca, N. Y., June-Sept., 1954-56 (H. E. Evans, C. S. Lin).

Oxybelus quadrinotatus Say (Plate XIX, figs. 105-106)

Body.—Length 8 mm.; maximum width 3 mm. Form as described and figured for *bipunctatus.*

Head.—Width .93 mm.; height .83 mm. Considerably more roughened by small convexities than in *bipunctatus.* Antennal orbits very small, circular, about 40 μ in diameter. Setae slightly more abundant than in *bipunctatus,* the longest ones about 60 μ in length.

Mouthparts.—Labrum .36 mm. wide, the apical margin prominently emarginate, the disc with about 20 strong setae (fig. 105). Epipharynx essentially as in *bipunctatus,* the spinules toward the base medially not quite as strong. Mandibles .41 mm. long, .22 mm. wide at the base, as described and figured for *bipunctatus.* Maxillae somewhat more broadly rounded and less strongly papillose than in *bipunctatus,* but otherwise very similar; palpi 50 μ long; galeae very short, only about 20 μ long. Labium with the palpi 55 μ long, the spinnerets 100 μ long, very slender and narrowly truncate apically; oral surface papillose and with paired patches of long spines (fig. 106).

Material.—Three specimens from Ithaca, N. Y., June-July 1955 (H. E. Evans).

Oxybelus melancholicus Chevrier

The larva of this European species has been described by Grandi (1929, Boll. Lab. Ent. Bologna, 2: 279-282). The head capsule, clypeus, and labrum appear to have many more setae than in the American forms. The labrum is weakly emarginate apically; the epipharynx is spinulose, with a large area medio-apically covered with papillae. The mandibles have five teeth and are essentially as described for *bipunctatus*. The lacinial area and the oral surface of the labium are not described in detail. The spinnerets are stout and blunt.

Oxybelus argentatus Curtis

Grandi (1954, Boll. Lab. Ent. Bologna, 20: 193-196) has recently provided a description and an excellent series of figures of this species. The body form is much as in the American species, with the anal segment forming a rounded lobe. The head is slightly wider than high and bears numerous setae. The mandibles are bidentate apically and have several small, blunt teeth on the inner margin. The lacinial area bears both papillae and spinules. The spinnerets considerably exceed the labial palpi and are blunt apically.

Explanation of Figures

In the drawings of the head, the anterior aspect is shown on the left side, the posterior aspect on the right side. In drawings of the labrum, the upper surface is shown on the left side, the under surface (epipharynx) on the right side. Drawings of the mandibles are of the dorsal (anterior) aspect unless otherwise stated; in drawings of the lateral aspect of the mandibles, the left mandible is always shown.

Plate IX

Fig. 1.—*Aphilanthops frigidus* (Smith), head.
Fig. 2.—Same, head and prothorax (lateral view).
Fig. 3.—Same, body (lateral view).
Fig. 4.—Same, labrum and epipharynx.
Fig. 5.—Same, mandible.
Fig. 6.—Same, antenna.
Fig. 7.—Same, portion of integument of prothorax, highly magnified.
Fig. 8.—Same, apex of labium (upper or oral surface, right half).
Fig. 9.—Same, apex of maxilla.
Fig. 10.—Same, spiracle.

Plate X

Fig. 11.—*Philanthus gibbosus* (Fabricius), apex of maxilla.
Fig. 12.—Same, mandible.
Fig. 13.—Same, body.
Fig. 14.—Same, labrum and epipharynx.
Fig. 15.—Same, spiracle.
Fig. 16.—*Philanthus solivagus* Say, labrum and epipharynx.
Fig. 17.—Same, antenna.
Fig. 18.—Same, apex of maxilla.

Plate XI

Fig. 19.—*Philanthus bilunatus* Cresson, labrum and epipharynx.
Fig. 20.—*Philanthus politus* Say, labrum and epipharynx.
Fig. 21.—*Cerceris fumipennis* Say, apex of maxilla.
Fig. 22.—Same, head.
Fig. 23.—Same, body.
Fig. 24.—Same, spiracle.
Fig. 25.—Same, labrum and epipharynx.
Fig. 26.—Same, apex of labium (oral surface, right half).

Plate XII

Fig. 27.—*Cerceris nigrescens* Smith, labrum and epipharynx.
Fig. 28.—Same, antenna.
Fig. 29.—Same, mandible.
Fig. 30.—*Cerceris robertsonii* Fox, labrum and epipharynx.
Fig. 31.—*Cerceris clypeata* Dahlbom, labrum and epipharynx.
Fig. 32.—*Eucerceris flavocincta* Cresson, head.
Fig. 33.—Same, last two segments of abdomen (lateral view).
Fig. 34.—Same, labrum and epipharynx.
Fig. 35.—Same, apex of maxilla.

PLATE XIII

Fig. 36.—*Trypoxylon clavatum* Say, head.
Fig. 37.—Same, antenna.
Fig. 38.—Same, spiracle.
Fig. 39.—Same, body.
Fig. 40.—Same, mandible.
Fig. 41.—Same, labrum and epipharynx.
Fig. 42.—Same, apex of maxilla.
Fig. 43.—Same, apex of labium (oral surface).

PLATE XIV

Fig. 44.—*Trypoxylon johannis* Richards, labrum and epipharynx.
Fig. 45.—Same, antenna.
Fig. 46.—Same, apex of maxilla.
Fig. 47.—*Trypoxylon arizonense* Fox, labrum and epipharynx.
Fig. 48.—Same, antenna.
Fig. 49.—*Trypoxylon spinosum* Cameron, labrum and epipharynx.
Fig. 50.—*Trypoxylon tridentatum* Packard, labrum and epipharynx.
Fig. 51.—Same, antenna.
Fig. 52.—Same, apex of maxilla.
Fig. 53.—*Trypoxylon politum* Say, labrum and epipharynx.
Fig. 54.—Same, antenna.
Fig. 55.—*Trypoxylon striatum* Provancher, labrum and epipharynx.

PLATE XV

Fig. 56.—*Trypoxylon aldrichi* Sandhouse, labrum and epipharynx.
Fig. 57.—Same, antenna.
Fig. 58.—Same, body.
Fig. 59.—*Trypoxylon frigidum* Smith, labrum and epipharynx.
Fig. 60.—Same, apex of labium.
Fig. 61.—*Trypoxylon adelphiae* Sandh., labrum and epipharynx.
Fig. 62.—*Trypoxylon politum* Say, spiracle.
Fig. 63.—*Trypoxylon rubro-cinctum* Packard, mandible.
Fig. 64.—*Pison* sp., labrum and epipharynx.

PLATE XVI

Fig. 65.—*Pison argentatum* Shuckard, head.
Fig. 66.—Same, spiracle.
Fig. 67.—Same, apex of maxilla.
Fig. 68.—Same, labrum and epipharynx.
Fig. 69.—*Crossocerus ambiguus* (Dahlbom), labrum and epipharynx.
Fig. 70.—Same, apex of labium.
Fig. 71.—Same, body.
Fig. 72.—Same, mandible.
Fig. 73.—Same, apex of maxilla.
Fig. 74.—Same, antenna.

Plate XVII

Fig. 75.—*Anacrabro ocellatus* Packard, head.
Fig. 76.—Same, spiracle.
Fig. 77.—Same, antenna.
Fig. 78.—Same, body.
Fig. 79.—Same, labrum and epipharynx.
Fig. 80.—Same, mandible (lateral view, posterior margin to left).
Fig. 81.—Same, portion of integument of prothorax, highly magnified.
Fig. 82.—Same, mandible (anterior view).
Fig. 83.—Same, apex of maxilla.
Fig. 84.—Same, apex of labium (oral surface).

Plate XVIII

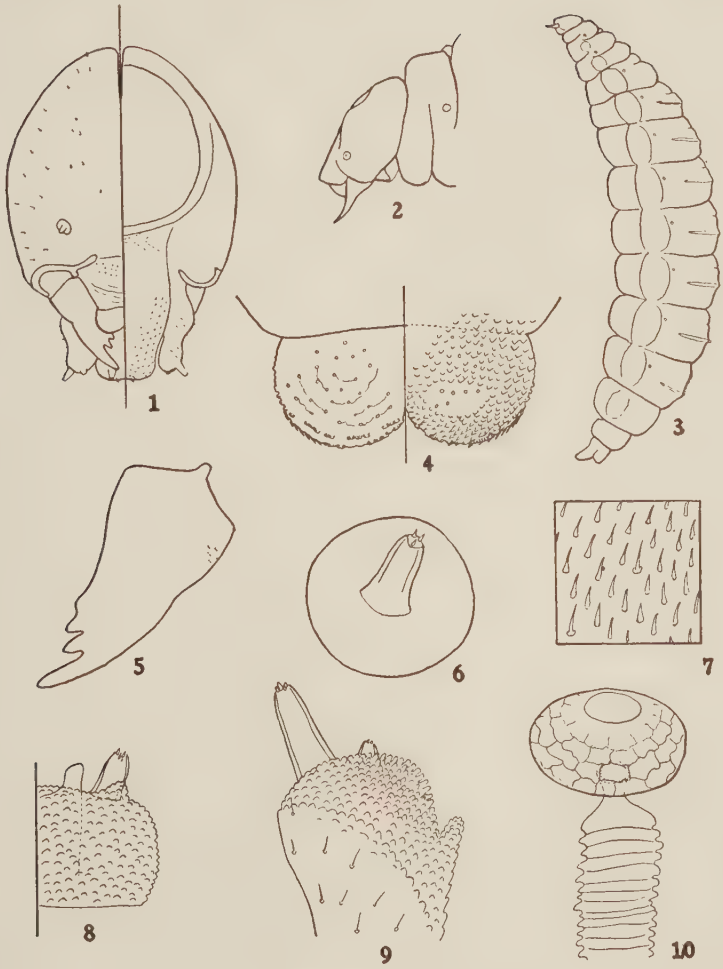
Fig. 85.—*Ectemnius stirpicolus* (Packard), head.
Fig. 86.—Same, spiracle.
Fig. 87.—Same, mandible (anterior view).
Fig. 88.—Same, mandible (posterior or ventral view).
Fig. 89.—Same, mandible (lateral view, posterior margin to right).
Fig. 90.—Same, labrum and epipharynx.
Fig. 91.—*Ectemnius atriceps* (Cresson), labrum and epipharynx.
Fig. 92.—Same, apex of maxilla.
Fig. 93.—Same, apex of labium.
Fig. 94.—Same, antenna.

Plate XIX

Fig. 95.—*Crabro advenus* Smith, labrum and epipharynx.
Fig. 96.—Same, mandible (lateral view, posterior margin to left).
Fig. 97.—*Crossocerus fergusoni* Pate, mandible (lateral view).
Fig. 98.—Same, spiracle.
Fig. 99.—*Euplilis arapaho* Pate, labrum and epipharynx.
Fig. 100.—Same, mandible (anterior view).
Fig. 101.—Same, mandible (lateral view).
Fig. 102.—Same, apex of maxilla.
Fig. 103.—Same, apex of labium (oral surface).
Fig. 104.—*Euplilis pedicellatus* (Packard), labrum and epipharynx.
Fig. 105.—*Oxybelus quadrinotatus* Say, labrum and epipharynx.
Fig. 106.—Same, apex of labium (upper or oral surface on right, lower on left).

PLATE XX

Fig. 107.—*Oxybelus bipunctatus* Olivier, head.
Fig. 108.—Same, spiracle.
Fig. 109.—Same, body.
Fig. 110.—Same, portion of integument of prothorax, highly magnified.
Fig. 111.—Same, labrum and epipharynx.
Fig. 112.—Same, apex of labium (upper or oral surface on right, lower on left).
Fig. 113.—Same, apex of maxilla.
Fig. 114.—Same, mandible (anterior view).
Fig. 115.—Same, mandible (lateral view, posterior margin to left).



Aphilanthops frigidus (Smith)

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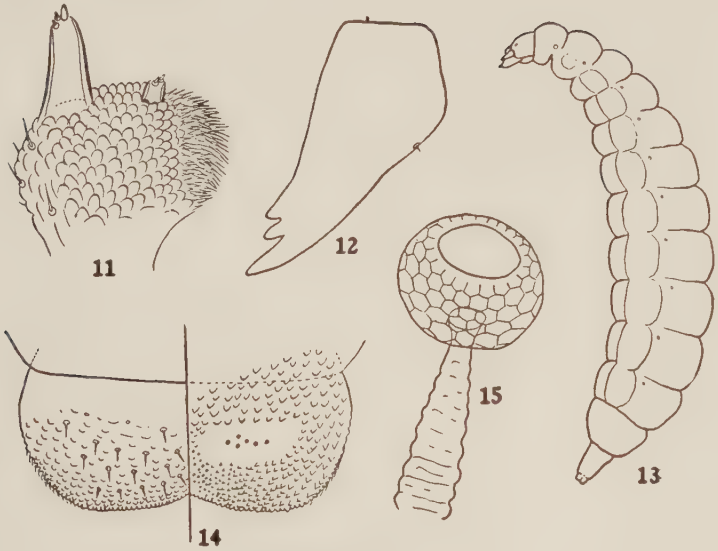
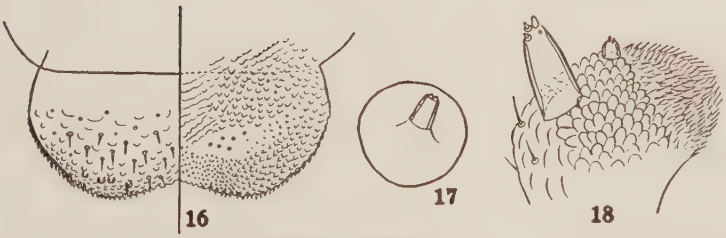


Philanthus gibbosus (Fabricius)



Philanthus solivagus Say

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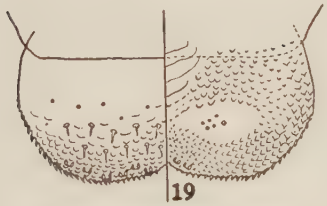
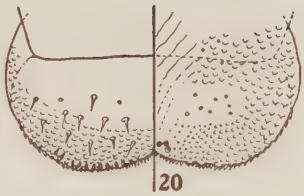
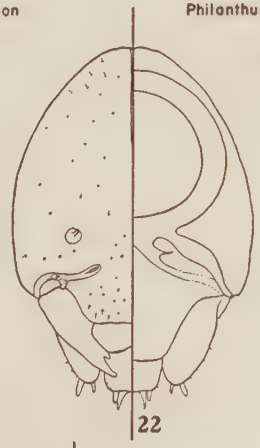
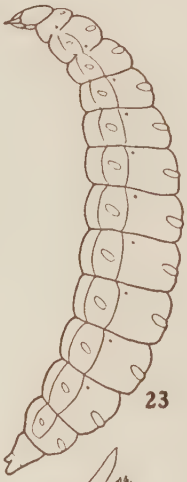


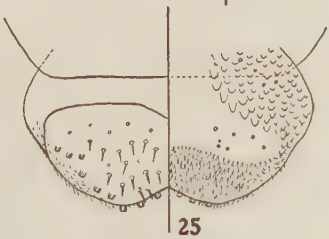
Philanthus bilunatus Cresson



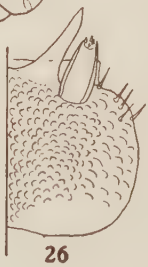
Philanthus politus Say







Cerceris fumipennis Say



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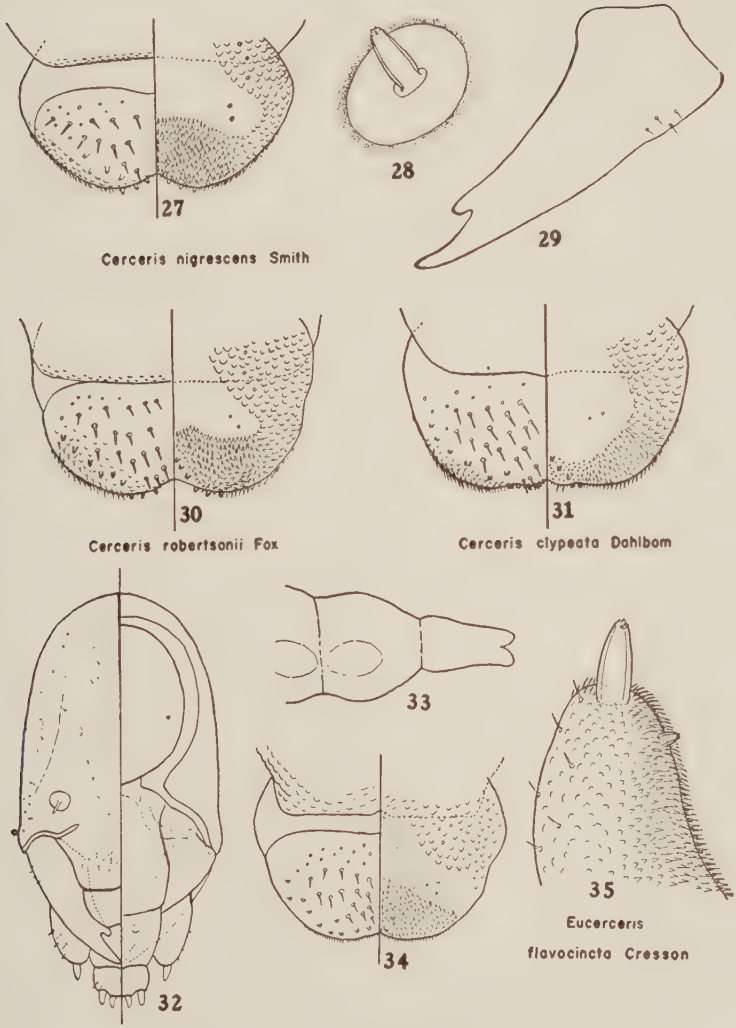

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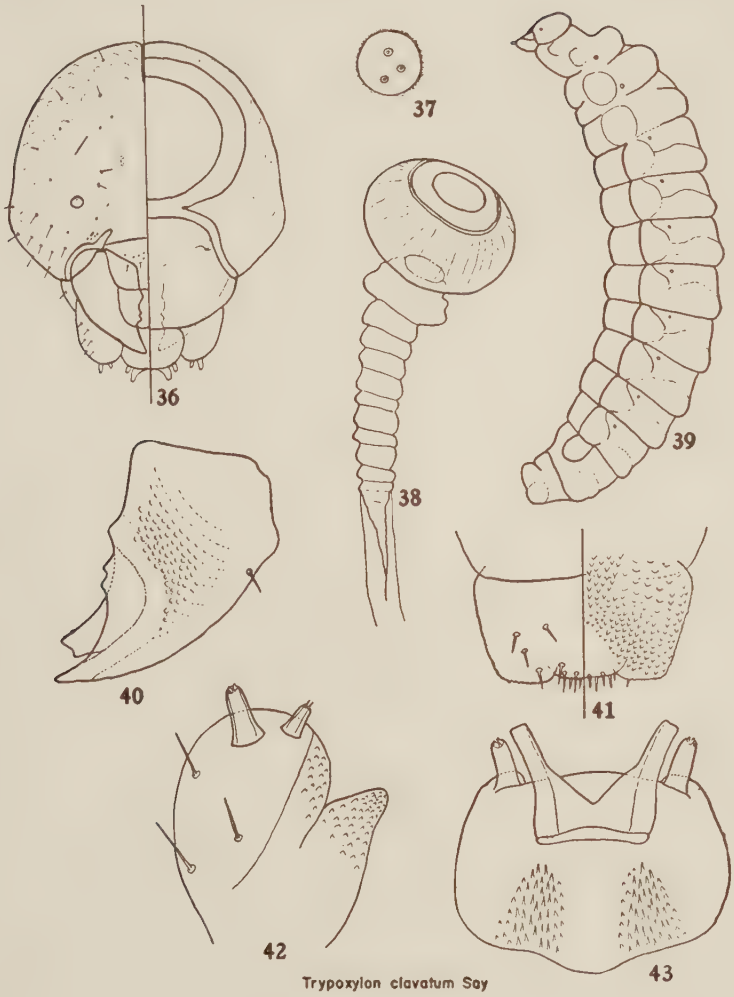

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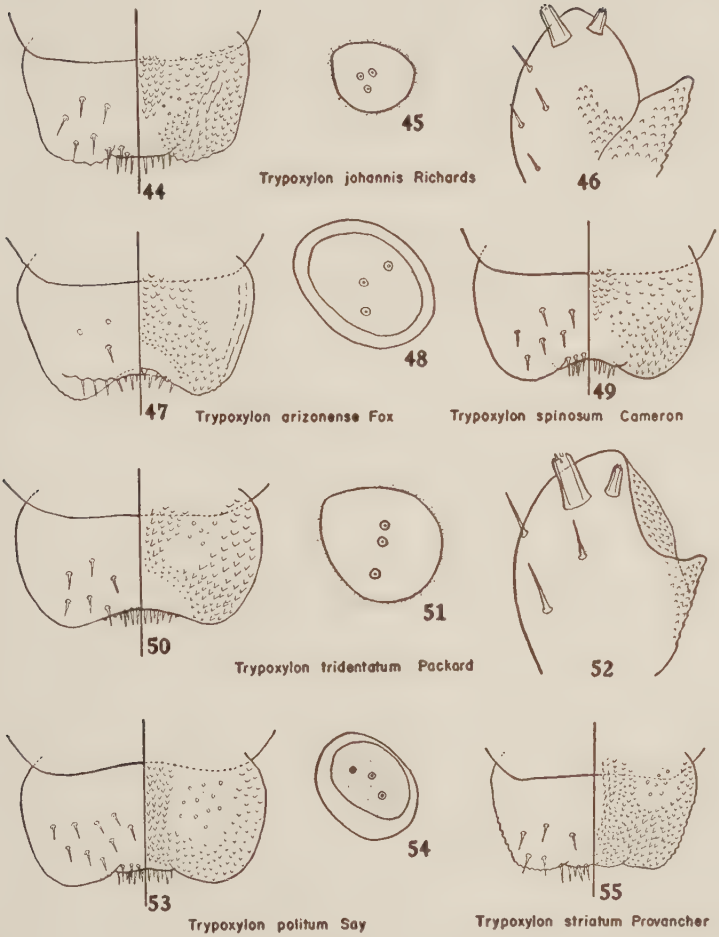

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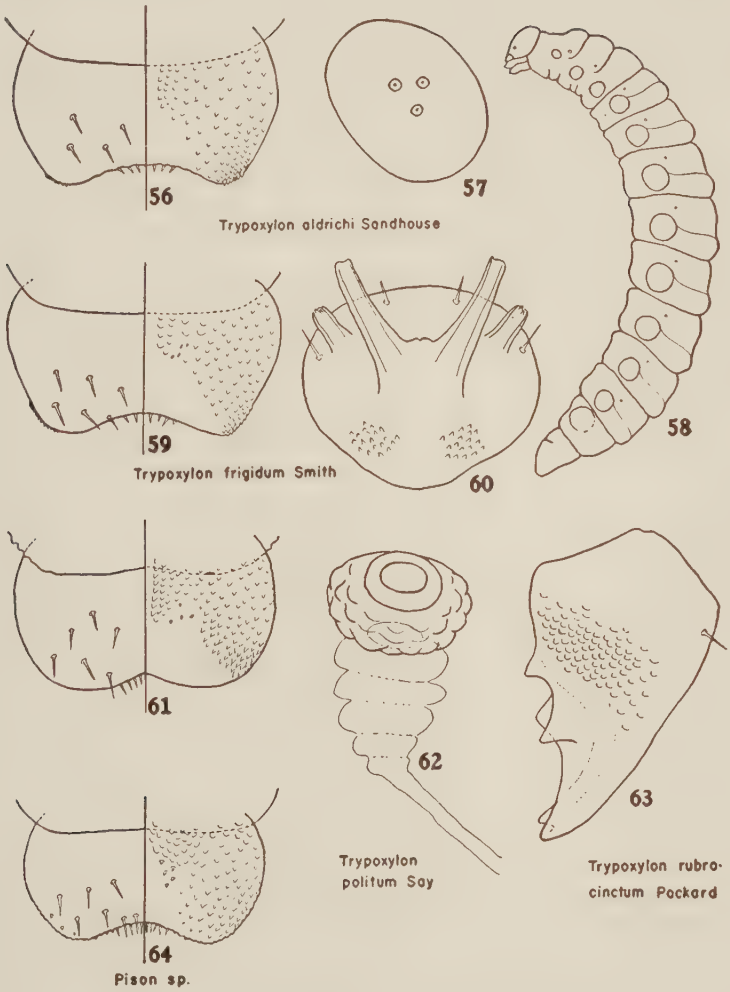

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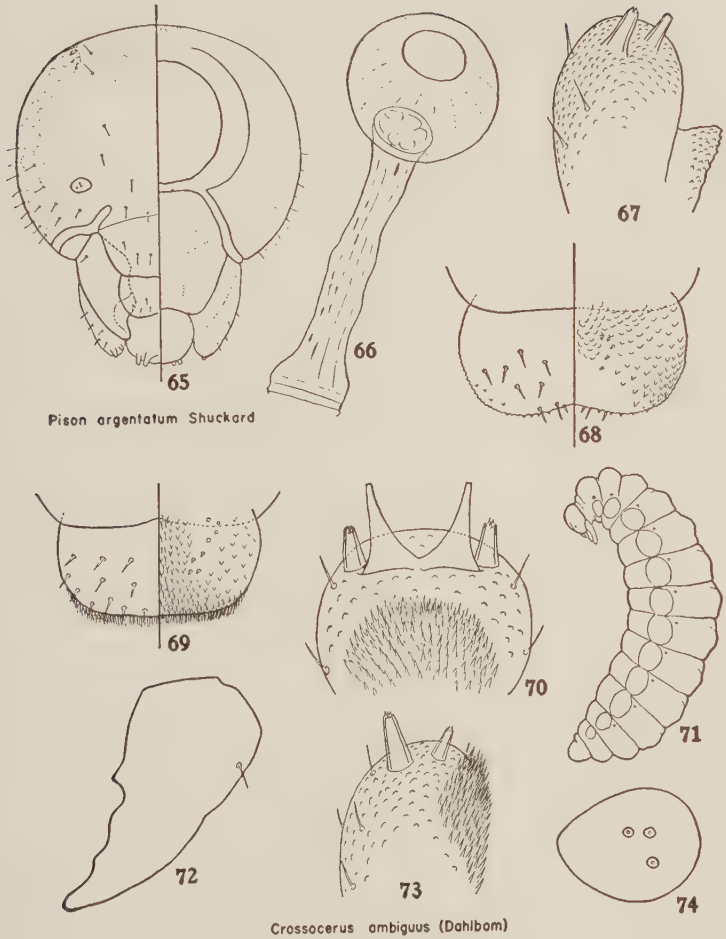

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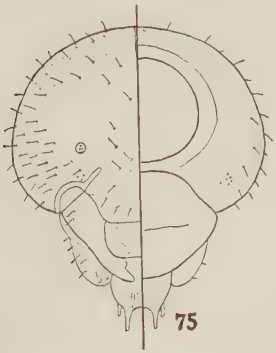

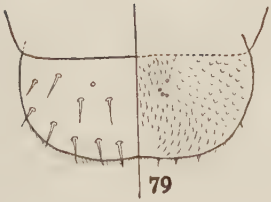

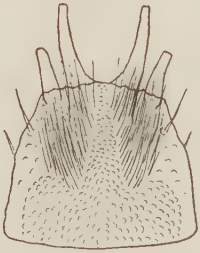

Anacrabro ocellatus Packard

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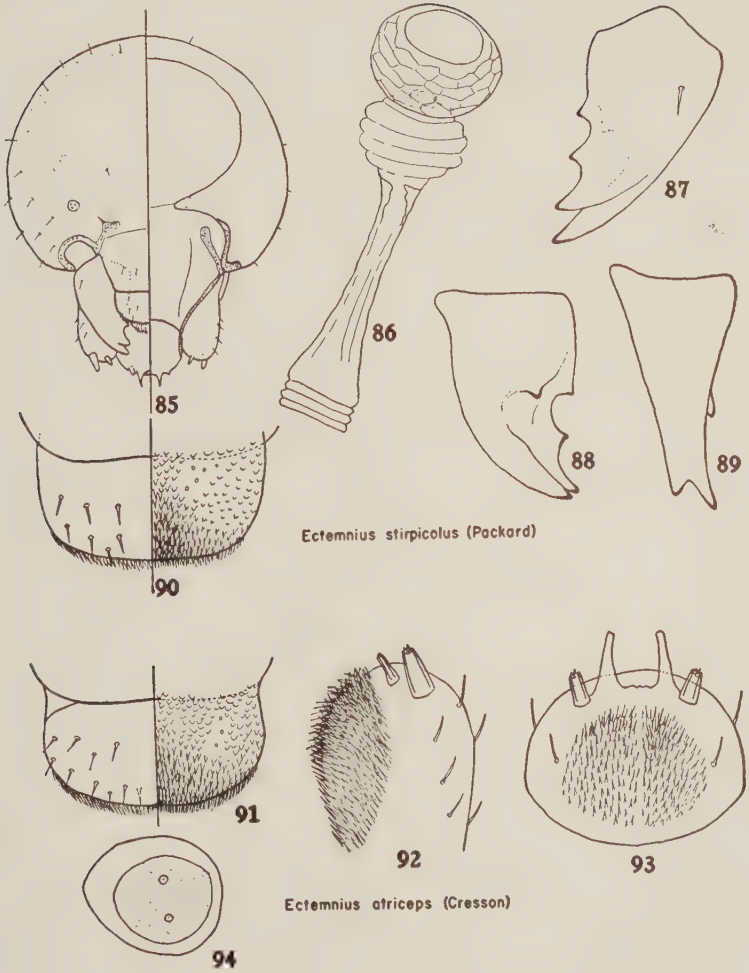

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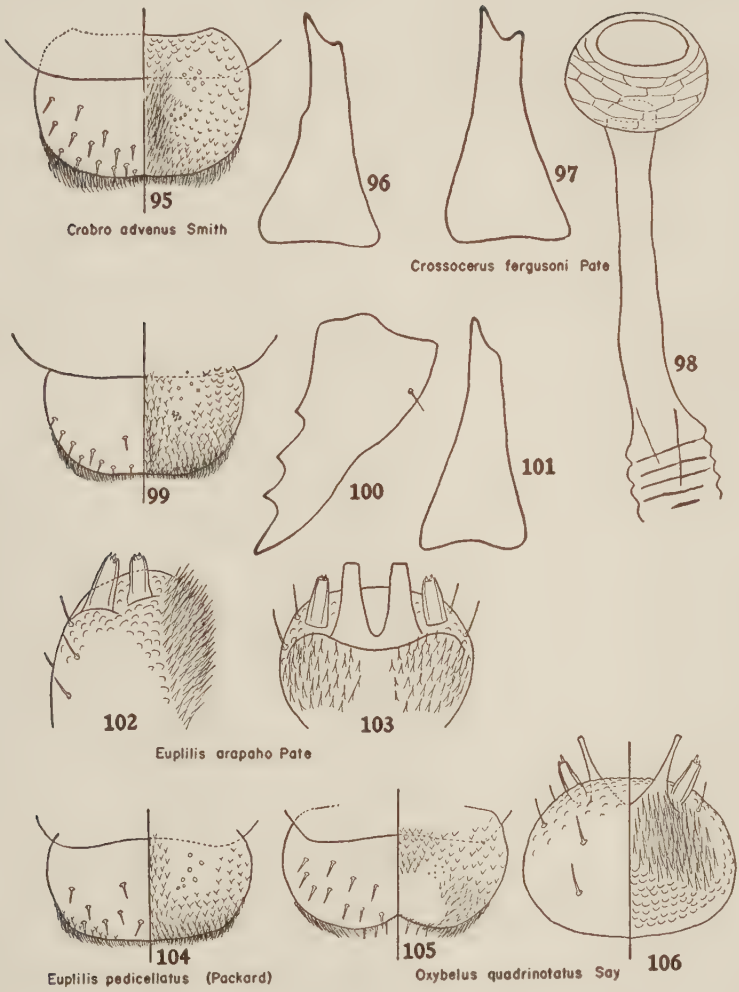

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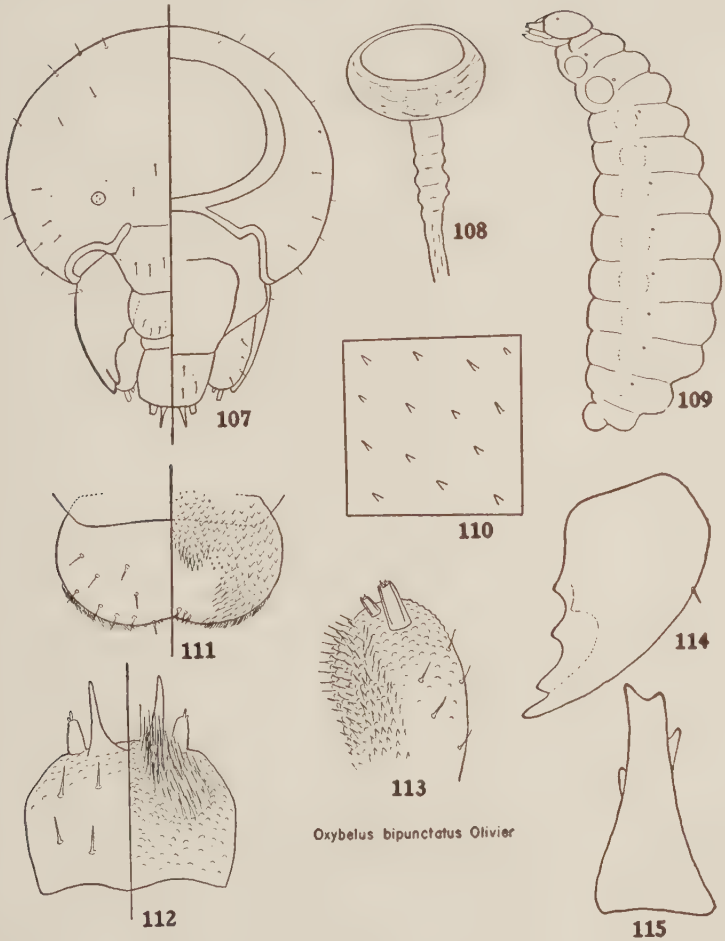

EVANS: LARVAE OF DIGGER WASPS

THE NERVOUS SYSTEM OF THE MILKWEED BUG, ONCOPELTUS FASCIATUS (DALLAS) (HETEROPTERA, LYGAEIDAE) *

ARNE SEMB JOHANSSON
Zoological laboratory, University of Oslo

Introduction

The milkweed bug, *Oncopeltus fasciatus* (Dallas), sometimes called the large milkweed bug, is increasingly used as a laboratory insect. As early as 1901 Montgomery, and later Wilson (1912) made cytological studies on this species, and during recent years many additional papers dealing with it have been published. Various aspects of the biology of *Oncopeltus* have been treated by Andre (1934) Niswander (1951), and Frings and Peissner (1952). The embryology has been studied by Butt (1949), and other aspects of the growth and development of this insect by Novák (1951, 1954, 1955), Bliss and Beard (1954), and Lin, Hodson and Richards (1954) have been worked on. It has also been the subject of other physiological problems (e.g., Frings, Goldberg and Arentzen, 1948; Auclair and Patton, 1950; Collias, McShan and Lilly, 1952; Clark and Craig, 1953), and has been found useful in the testing of insecticides (e.g. Beard, 1952; Grayson, 1953).

Our knowledge of the structure of this insect, while steadily increasing, is still fragmentary and lacking in many ways. The reproductive organs are among the best known organ systems, thanks to a series of recent papers (Bonhag and Wick, 1953; Bonhag, 1955 a, b; Wick and Bonhag, 1955). Information is also available on the digestive system (Hood, 1937), the mouthparts (Butt, 1943), the maxillary, glands (Linder and Anderson, 1955), and the prothoracic glands (Wells, 1954). Recently the gross anatomy of the nervous system of *Oncopeltus* has been treated by Rutschky and Stryjak (1955).

* Publication of this study was made possible by a grant from the Grace H. Griswold Fund of the Entomology Department of Cornell University.

Other papers have been written containing information on the nervous system of other Hemiptera. Pflugfelder (1936-37) who used the Golgi method extensively, gives the most valuable description of the neurohistology of the brain of various representatives of this order. This study contains additional information on this organ system mainly intended to serve as a background for experimental work now in progress. Besides providing a description of the anatomy and histology of the nervous system of the imago, it furnishes an analysis of some of the changes during postembryonic development.

Material and Methods

The material for this study was taken from a laboratory colony of the milkweed bug, *Oncopeltus fasciatus* (Dallas), originally supplied from Cornell University. The breeding was carried out in the way described by Butt (1949). However, laboratory conditions varied somewhat in the course of the work. The temperature ranged approximately from 18 to 22 ° C, while the relative humidity was between 40 and 50% in winter and between 60 and 80 in summer. Adult females were able to survive for 25-26 weeks, and males even longer.

The anatomy of the nervous system was studied by dissection of preserved specimens and the data obtained were checked on sectioned material. For general histological purposes the material was fixed in alcoholic Bouin's solution and stained in various hematoxylins (Heidenhain, Ehrlich or Delafield) mostly with eosin as counterstain. For the study of neurosecretory activity the material was fixed in aqueous Bouin's or Helly's fluid and stained according to Masson-Foote, with Gomori's chrome hematoxylin phloxin, or Gomori's aldehyde fuchsin as modified by Halmi (1952) and Dawson (1953). The Masson-Foot technique also proved very satisfactory for general purposes and for the study of the connective tissue sheaths. Among silver impregnations the Golgi method, as used by Pflugfelder (1936-37), gave good results in the adult bug. Altogether 330 specimens were treated by this method. The Bodian protargol technique, as modified by Power (1943) and Rogoff (1946), was tried after the following fixatives; aqueous and alcoholic Bouin,

Carnoy, Dietrich, Petrunkewitch (with 25% formalin). Protargol from both German (Bayer) and American firms (Winthrop Chemical Company) was used. Although the method has been successful with *Drosophila melanogaster,* the results with the milkweed bug did not come up to expectations, nor did Meyer (1951) obtain positive results with the protargol method in various Rhynchota. Thus the detailed study of fiber tracts must await the development of methods which prove more successful in the Heteroptera.

The material was usually embedded in tissuemat or paraffin and sectioned at 7 or 10 μ. For Golgi preparations thicker sections (15-20 μ) were prepared. Whenever the central nervous system was not dissected out before fixation, the embedding was done through methylbenzoate-celloidin.

The volumetric measurements were carried out by means of camera lucida drawings of sectioned material at known magnifications, and a planimeter. The results (tables 1-4) are based on measurements from two specimens in each group. The method and its limitations are described by Hanström (1926) and Ratzerdorfer (1952).

The Anatomy of the Nervous System

The central nervous system of the Hemiptera shows a strong, but somewhat varying degree of concentration of the ganglia (Brandt, 1878; Pflugfelder, 1936-37). *Oncopeltus* and other investigated members of the family Lygaeidae have four separate ganglionic masses (fig. 44): the supraoesophageal ganglion usually called the brain (BRN), the suboesophageal ganglion (SGN), the first thoracic ganglion (I THGN), and one composite ganglion (LGN) containing the second and third thoracic ganglia plus all the abdominal ganglia.

The brain and the suboesophageal ganglion are situated in the head(fig. 1). They are so closely connected by the short and thick circumoesophageal connectives that they look like a single mass of nervous tissues surrounding the oesophagus. The brain consists of three usual parts: proto-, dueto- and tritocerebrum. In a dorsal view, the protocerebrum covers most of the two other parts (fig. 4). The two halves of the protocerebrum are separated dorsally by a slight median depression. Laterally the

optic lobes are easily distinguished (fig. 4; LO). The optic nerves (NO) connect the more anterior compound eyes to the optic lobes.

The term " optic nerve " is used in this paper for the postretinal fibers connecting the compound eyes with the optic lobes. The term sometimes designates the fibers connecting the optic ganglia and the central parts of the brain (see Pflugfelder, 1936-37, p. 7, and Roonwal, 1937, p. 216).

Each of the two ocelli is connected with the protocerebrum by a short stalk (figs. 2 and 4; OS), which reaches the brain in its dorsal part. From the posterior part of the protocerebrum two nerves, for the most part fused, (nervi corporis cardiaci I and II. (figs. 1, 4, and 36; NCC I and II)) connect the brain on each side with the corpora cardiaca-allata.

The deutocerebrum is well developed and can be separated from the protocerebrum as an anterior projection on each side of the brain (fig. 4; DCS). The triticerebrum is difficult to distinguish externally. The antennal nerves (figs. 2, 3, and 4; NANT) arise from the anterior part of the deutocerebrum. They contain both motor and sensory fibers and are well developed in accordance with the great importance of the olfactory sense in the Gymnocerata. Smaller motor branches (figs. 3 and 4) are formed laterally from the antennal nerve before it turns and enters the antenna. The labro-frontal nerves depart from the brain medially to the antennal nerves, but the fibers can be traced back to the more ventral tritocerebrum. They each divide into one labral nerve (figs. 2 and 4; NLBR) which goes in an anterior direction, and one frontal nerve which is short and thick and fuses with the nerve from the opposite side in the frontal ganglion (figs. 1 and 4; GFR). From the frontal ganglion, situated anteriorly to the dilator muscles of the pharynx, the unpaired procurrent nerve (Dönges, 1954; frontal nerve Rutschky and Stryjak, 1955) goes forward (figs. 1 and 4; NP), while the unpaired recurrent nerve (fig. 4; NR) passes posteriorly above the oesophagus. A commisure (fig. 1; FRC) leaves the brain a little posteriorly to the labro-frontal nerve and connects the two halves of the brain ventrally to the pharynx.

A small nerve (figs. 1 and 36; NTR) arises on each side from the posterioventral part of the brain and fuses with the NCC I and II. Although its origin in the milkweed bug has not been determined with certainty, it can probably be compared with the tritocerebral branch of the nerves to the corpora cardiaca-allata described by Pflugfelder (1936-37, p. 60) and Cazal (1948, p. 93).

The suboesophageal ganglion which lies a little posterior to the brain, consists of the three pairs of ganglia which innervate the mouth parts. Externally they can only be identified by their nerves, all of which are paired (fig. 1). The main branches of the mandibular nerves are shown in figs. 3 and 5 (NMD). The first maxillary nerve (figs. 3 and 5; NMX_1) runs in the form of a flat band to the retractor of the maxilla. One branch of this nerve that extends forward between the maxilla and the mandible, seems to be partly associated with the latter. The main branches of the second maxillary nerve are shown in figs. 2 and 6 (NMX_2). The third maxillary nerve described by Graichen (1936) in *Nepa cinerea* as going to the "Mandibeltasche" (maxillary sac?), in the milkweed bug seems to be a branch of the second nerve. A fourth nerve which may be regarded as a branch from the second maxillary nerve (figs. 1, 5, and 36; NLA), moves in *Oncopeltus* dorsally and posteriorly and seems to fuse with the nerves to the corpora cardiaca-allata. Perhaps it corresponds to the lateral nerve which in the Cryptocerata connects the mandibular nerve and the corpora cardiaca-allata (Cazal, 1948).

The strong labial nerves are shown in fig. 1 (NLB). One pair of nerves innervating inter alia the salivary glands arises from the posterior part of the suboesophageal ganglion (fig. 1; NSG). The main branches of this nerve pass laterally and posteriorly to form a chiasma with the first prothoracic nerve.

The prothoracic ganglion which lies in the ventral part of prothorax, is illustrated in fig. 7. It is distinctly separated from the suboesophageal ganglion and the last ganglion by pairs of connectives. The ventral side of the ganglion is convex, the dorsal side rather flat. It has four pairs of nerves, the main

branches of which are shown in figs. 7, 8 and 9. The nerves to the legs (fig. 7; NPT_3) which are the largest ones, have a smaller dorsal branch. The small ventral nerves (fig. 7; NPT_4) probably correspond to the sternal nerves found by Holste (1910) in *Dytiscus*.

The last ganglion (central ganglion, Rutschky and Stryjak, 1955) lies in the ventral part of the mesothorax (figs. 10 and 15). It is larger than the first thoracic ganglion and more elongate in shape. Anteriorly it is fastened to the furca of the prothorax by ligaments. The nerves from the last ganglion are diagrammatically shown in fig. 16. The four pairs of nerves of the mesothorax appear in figures 10, 11, and 12. As in the prothorax, the largest ones are those to the legs (fig. 12; NMT_3). Also in the mesothorax a pair of small sternal nerves springs from the ventral surface of the ganglion (fig. 10; NMT_4).

The nerves of the metathorax are shown in figures 13 and 14. The first pair of nerves ($NMAT_1$) innervates the wings and the flight muscles, as do the corresponding nerves of the mesothorax (figs. 10, 11, and 12; NMT_1). The second pair of nerves (fig. 14; $NMAT_2$) seems to correspond to the last three pairs of nerves of the mesothorax.

The abdomen of the milkweed bug consists of 11 segments (Bonhag and Wick), 1953), but only seven pairs of nerves are present (figs. 15 and 16), the largest of which are the genital nerves (fig. 15; NAB_7). The first pair (fig. 13; NAB_1) innervates muscles which are situated between the metathorax and the abdomen and has to be considered as the nerves of the greatly reduced first abdominal segment. Similar conditions were found in *Nepa* by Hamilton (1931) and in *Nezara* by Malouf (1933). The abdominal nerves of the Heteroptera usually seem to be more fused than the corresponding nerves in *Oncopeltus*. Brandt (1878) in his illustrations of the nervous system of various Hemiptera shows that, except for the nerves to the first and second abdominal segments, the nerves are mostly concentrated in one pair. This is also the case in the one species of *Lygaeus* which he portrays. In *Nepa cinerea* Hamilton (1931) found a pair of stout nerves which, when sectioned, proved to contain fibers of five small nerves. The first four pairs of abdominal

nerves have separate origins from the ganglion in *Nezara* (Malouf, 1933), while in *Syromastes marginatus*, only three pairs of nerves from the abdominal ganglia are present, (Pflugfelder, 1936-37). In *Naucoris cimicoides* nine pairs of abdominal nerves are fused in two pairs of nerve bundles (Rawat, 1939). Individual variations which have been found in the nervous pattern in other insects (Hertweck, 1931; Dönges, 1954), were also observed in the milkweed bug.

The Histology of the Brain

1. The Protocerebrum

The optic lobes (lobi optici).—The optic lobes will be treated here as parts of the protocerebrum. Each optic lobe consists of three ganglionic bodies, a distal lamina ganglionaris, a median medulla externa, and a proximal medulla interna, which are more or less surrounded by ganglion cells.

The retinal fibers, after having penetrated the basement membrane of the eye, form small bundles. Those which originate from the anterior part of the eye, are larger and bandlike (fig. 20a). In the Geocorisae with long optic nerves, Pflugfelder (1936-37) has observed that the fibers are arranged in a dorsal and a ventral part forming two distinct and separate bundles. This is the case in nearly all the Pentatomidae and in the two Lygaeidae which he examined, while in the Coreidae, where the optic nerves are shorter, they consist of a single tract of retinal fibers. In *Oncopeltus* the optic nerves are not divided into a dorsal and a ventral part (fig. 20a). As shown by Pflugfelder, the optic nerves in the Lygaeidae are shorter than those of the Pentatomidae, and more like those of the Coreidae. The fusion of the fibers into one main nerve in the milkweed bug thus reflects the resemblance with the Coreidae.

The lamina ganglionaris (figs. 17b and 18a; LG) has the shape of the flat head of a mushroom with the convex side directed anteriorly and laterally. It is longer in the horizontal direction than in the dorso-ventral. The lamina ganglionaris shows no stratification in contrast to the two other optic bodies. Its distal part, however, is characterized by a palisade structure. In cross-sections it looks like a sieve (fig. 20c). The outer cellular

part is especially well developed dorsally. From this part more or less regular rows of cells descend between the retinal fibers (fig. 17b, c; LGC, and fig. 20b). According to Pflugfelder (1936-37) the outer cellular part contains two types of neurones: each, after having given off collaterals to the lamina ganglionaris, ends in the medulla externa (fig. 22; nos. 2 and 3). Both of these types have also been observed in *Oncopeltus*. A difference in the appearance of the perikaryons of the outer neurons corresponding to these two types has not been observed.

The fibers reach the medulla externa by way of the chiasma externum (fig. 18a; CHE). The medulla externa is the largest association center in the optic lobe (figs. 17a, b and 18a, b; ME). It is ovoid in shape with the proximal part absent, giving space to the medulla interna. In sections the medulla externa shows a laminated structure, the layers following the convex surface. Three dark staining parts separated by lighter stained areas are easily identified as follows: a dorsal and distal part, well developed with distinct cross-striation; a thinner median part; and a proximal, more ventral part. These three main parts are composed of layers of different staining qualities. Depending upon the fixation and staining procedure it is possible to identify up to ten layers, as has also been found by Graichen (1936) and Pflugfelder (1936-37) in other Heteroptera.

The globuli cells are small, the nuclear diameter being 4-5 μ. They are situated both dorsally and ventrally to the association body. Some cells, slightly larger, are situated at the anterior border between the medulla externa and interna (fig. 22; no. 8).

In the medulla externa we find the endings of the two types of cells from the lamina ganglionaris, the type A of Pflugfelder in the middle zone, and the type B in the outer zone (fig. 22; nos. 2 and 3). Of these, type B shows up best in the milkweed bug. Most of the globuli cells of the medulla externa send their axons through the body, give off collaterals, and end in the medulla interna (fig. 22; no. 5). These were only rarely impregnated with the Golgi method in *Oncopeltus*. The cells which were most frequently impregnated in this species were the unipolar T-cells, which, being situated at the lateral border between medulla externa and interna, send one branch into the

inner or median zone of the medulla externa, while another branch goes to the medulla interna (fig. 22; no. 6). Pflugfelder (1936-37) has found still another cell type connecting the medulla externa and interna (fig. 22; no. 7). It occurs rarely in the specimens studied by Pflugfelder and has not been identified at all in the milkweed bug. The larger of the cells mentioned above (fig. 22; no. 8) give off a large branch which forms the so-called horizontal fibers of the medulla externa. Another branch from these cells forms the tractus opticus posterior which connects the medulla externa with other parts of the brain (fig. 21; no. 4).

Fibers from the medulla externa form the chiasma internum before they enter the medulla interna. The medulla interna (figs. 17a and 18c; MI) which is pear-shaped, can easily be divided into two parts: a larger part distal to the posterior optic tract and a smaller part proximal to it, and separated from the outer part by a more open zone. Both parts have a more or less stratified structure and, according to Pflugfelder (1936-37), it is possible in the Hemiptera to separate three main zones in the distal part so one can distinguish altogether four main zones.

The cells around the distal part of the medulla interna are typical globuli cells of about the same shape and size as those around the medulla externa, while the proximal part is surrounded by slightly larger cells. Of the different processes observed in Golgi preparations, those from the unipolar T-cells (fig. 22; no. 6) have already been mentioned. Of the other cells, those marked as nos. 5 and 11 in figure 22 were rarely impregnated.

The connections between the optic lobes and the protocerebrum are formed by several distinct fiber tracts. The tractus opticus posterior (fig. 21; no. 4) is the largest. It extends from the medulla externa in a ventral direction, anterior to the medulla interna, bends posteriad, and follows the border between the neuropile and the cellular cortex until it ends in the median part of the protocerebrum, ventrally and anteriorly to the bridge (fig. 18f; TROP).

The other fiber tracts extend from the medulla interna. Of these the tractus opticus anterior is easily observed (fig. 17a; TROA, and fig. 21; no. 1). It runs dorsally to the tuberculum

opticum (fig. 21; TO), a small glomerulus in the anterodorsal part of the protocerebrum.

Of the other fiber tracts one (fig. 21; no. 2), which perhaps corresponds to the tractus opticus medialis interior, passes from the posterior part of medulla interna in a ventral and then median direction. After giving off one branch which seems to end in the accessory lobe, the main part passes above the stalk of the mushroom body to the median part of the protocerebrum. It ends close to the central body. Whether any connections to the central body, as found by Hanström (1928) in *Periplaneta*, are present or not, could not be determined. According to Pflugfelder (1936-37) the tractus opticus medialis inferior ends in the region behind the stalk of the mushroom body.

A third tract passes from the anterior part of medulla interna in a median and ventral direction and seems to end laterally to the roots of the mushroom body (fig. 21; no. 3). A tract corresponding to the tractus opticus medialis superior (Pflugfelder, 1936-37) ending in the dorsolateral parts of the protocerebrum, could not be found.

The mushroom bodies (corpora pedunculata).—Since the first description of the mushroom bodies in insects by Dujardin (1850), their degree of development has been taken as an indication of the psychic development of the insects. They are among the main association centers in the brain, and their morphology has been thoroughly studied. Flögel (1878) did not find the mushroom bodies in the Rhynchota, and Kenyon (1896) has mentioned only a few words about them. In his comparative study, Bretschneider (1913) has placed the Hemiptera with the Diptera and the dragonflies. They are all characterized by large central bodies and insignificant mushroom bodies. Hanström (1928) has given the first more detailed description of the mushroom bodies in the Hemiptera and found them better developed in the Gymnocerata than in the Cryptocerata. Graichen (1936) has described the conditions in *Nepa*, but it was not until the use of special techniques by Pflugfelder (1936-37) that the details of the structure of the mushroom bodies became known. The globuli cells are of two types: a small type of cell arranged in two groups which build up the dorsal glomerulus, and another

cell type which gives off collaterals to the ventral glomerulus. Besides processes from these cells, endings from the olfactory tract are found in the dorsal glomerulus, while the ventral glomerulus has connections to the motor deutocerebrum. Two types of connections between the roots of the mushroom bodies and the central body were found.

The mushroom bodies are paired association centers. Their position in *Oncopeltus* is indicated in figures 17, 18 and 19. They each consist of a dorsal glomerulus (fig. 21; CPD) and a much smaller ventral glomerulus, a stalk proceeding from these bodies in a ventroanterior direction, and an anterior root (fig. 21; CPR) in which the stalk ends. The dorsal and the ventral glomeruli are situated close together in the dorsoposterior part of the brain. The dorsal glomerulus is shaped like a kidney (figs. 17b, 18e, f, and 19b; CPD) whereas the ventral one is globular (figs. 17b and 18e; CPV). In sections the dorsal glomerulus looks like a single unit. The fibrous stalk which leaves from the hilus is, however, split into two parts (fig. 18e; CPS) which soon fuse to form one structure (fig. 18d; CPS). The stalk passes in an anterioventral, slightly median direction (figs. 17b and 19b; CPS). In the anteriomedial part of the protocerebrum, the stalk ends in a very complicated root system (figs. 17c and 18c; CPR). Two of the branches can be distinguished. The ramus superior (fig. 18d; CPRS) goes in a dorsal and partly posterior direction, medially and dorsally to the stalk, and ends dorsolaterally to the central body. Another branch, which is not so well developed, is the ramus posterior (fig. 18d; CPRP). This passes ventrally to the ramus superior and the stalk, posteriad to the anterior part of the central body.

The dorsal glomerulus is surrounded on the ventrolateral side by cells which form a single mass and are typical globuli cells with small, dark-staining nuclei (diameter 5-6 μ) and little cytoplasm. The cells in the ventral part are somewhat bigger and probably belong to the ventral glomerulus. The small globuli cells send their axons down the stalk. A branch is given off to the dorsal glomerulus, and the endings are found throughout the body indicating the unity of the glomerulus (fig. 23). In the root system the axon splits up, and according to Pflugfelder

(1936-37) the endings from one axon are found in all branches of the roots. The silver impregnations of the roots in the adult milkweed bug, however, did not yield pictures clear enough to allow a statement on the deails of the root structure. The cells forming the ventral glomerulus are of another type. They send several collaterals into this body while the axon extends down the stalk (figs. 23 and 24).

As a principal association center the mushroom bodies receive fibers from several other parts of the brain. The olfactory tract (fig. 21; no. 5), a well-developed fiber bundle, goes from the olfactory lobe in a dorsal and posterior direction, and reaches the median part of the dorsal glomerulus of the mushroom bodies. A short but strong tract connects the lateral parts of the dorsal glomerulus to the protocerebral lobes (fig. 21; no. 7). The ventral glomerulus is connected to the motor part of the deutocerebrum, a connection first described by Pflugfelder (1936-37). The roots are connected with the central body (fig. 21; no. 6). Some of the fiber endings from other parts of the brain, connecting the central body and the roots, are shown in figure 25.

The central body (corpus centrale).—The central body was first described in insects by Dietl (1876) and has played an important role in later descriptions of the insect brain. It consists of several bodies, and there is considerable confusion regarding the terminology even though the parts of the central body seem to be much the same in most insects.

The central body is considered to be an important association center. It has no special group of globuli cells, but it receives fibers from many parts of the brain. In the Geocorisae, Pflugfelder (1936-37) lists connections with the following parts: the bridge, the lateral and lateroposterior parts of the protocerebrum, the accessory lobes, the roots, the ramus superior and the glomeruli of the mushroom bodies, the deutocerebrum, and the tritocerebrum.

In *Oncopeltus* the central body consists of well-developed glomeruli in the median, central part of the brain (fig. 17b; CB). A dorsal body (fig. 19c; CBD) which is shaped like a thick horseshoe, with the arms extending forward and partly ventrad, embraces a smaller median, ellipsoid body (fig. 19c; CBV).

These two bodies form the main part of the central body. In addition we find on each side of the median line, posteriorly and ventrally to these bodies, a small glomerulus called the tubercle (fig. 19c; CBT).

The dorsal and ventral bodies are very closely connected. While the ventral body has a more homogeneous structure, the dorsal body is split in parts by fibers radiating out from the ventral body. In transverse sections it is sometimes possible to count ten such divisions of the dorsal body, but usually only eight are visible.

The central body is surrounded by a well-developed layer of fibers. It is impossible without successful impregnations to tell with certainty which of these fibers enters the body itself. The layer of fibers, however, has connections to several parts of the brain. Connections to the bridge are formed by the different bundles entering in the posterior part (fig. 21; no. 9). From the ventrolateral part fiber tracts pass to the lateral parts of the protocerebrum and the accessory lobes (fig. 21; no. 8 and 10). Connections to other parts of the central body could not be determined with certainty, nor was it possible to tell whether any collaterals from the tractus chiasmaticus which passes close to the central body anteriorly, enter it. A possible connection between the central body and the optic lobes is mentioned elsewhere. A schematic drawing of the different endings observed in the central body is given in fig. 25. Some fibers send their collaterals to both the ventral and the dorsal body, while others appear to invade the roots of the mushroom bodies as well as the ventral part of the central body. The special structure of the dorsal body is explained by the arrangement of fibers going through it at certain places. The branches of other neurons are found throughout the greater part of the bodies (figs. 26 and 27).

The protocerebral bridge (pons cerebralis).—Viallanes (1887), who was the first to describe this association center of the insect brain, thought that the bridge contained fibers from the ocellar stalks. Later it has often been considered as a center for the ocellar stalks or as an optical association center, because it also receives fibers from the optic lobes (Bretschneider, 1914). Pflugfelder (1936-37) could show that in the cicada *Dundubia*

no fibers from the ocellar stalks enter the bridge. This, in the Heteroptera, is for the most part built up by cells lying in the pars intercerebralis. These cells also form the connections to the central body. The bridge receives fibers from the posterior optic tract, the anterior part of pars intercerebralis, and the lateral parts of the protocerebral lobes.

In *Oncopeltus* the protocerebral bridge is a typical glomerulus, situated posteriorly to the central body close to the cells in the pars intercerebralis (figs. 17c, 18f, and 19c; BR). It has the shape of a wide open bow with the concave side downwards, and it is almost circular in cross-sections. It consists of two halves connected with a commisure across the median line (fig. 21; no. 14).

From the dorsal part of the bridge three short fiber tracts on each side form the connections with the central body (fig. 21; no. 9). The most lateral one bends ventrally and laterally around the olfactory tract. Another strong fiber tract passes close to the lateral sides of the bridge from cells in the pars intercerebralis (fig. 21; no. 12). Only some of the endings in the bridge were impregnated (fig. 28). According to Pflugfelder (1936-37), the perikaryon of the cell type characteristic of the bridge is situated in the pars intercerebralis. The collaterals ending in the bridge form a dense mesh of fibers, while the axons form connections to the central body and the protocerebral lobes.

The pars intercerebralis.—Haller (1905) has used the designation "pars intercerebralis" for the dorsomedial part of the brain situated between the mushroom bodies. The bridge divides it into an anterior and a posterior part which are connected by a strong median fiber tract. It was in this part of the brain that Weyer (1935) first described gland-like nerve cells in the honey bee. These neurosecretory cells which were later found in a great variety of insect species, among them the bug *Rhodnius* (Hanström, 1938), attracted attention when Wigglesworth (1939, 1940) showed that a hormone regulating molting fluid in *Rhodnius* is furnished by the dorsal half of the central mass of the brain.

In *Oncopeltus* the anterior part of the pars intercerebralis is occupied by a group of rather large neurons. They are situated between the caps of the mushroom bodies and dorsad to the

central body (figs. 17a and 29; PI). The cells are of various types and can be differentiated by a variety of histological methods. After fixation in Bouin's or Helly's fluid and staining in Gomori's aldehyde fuchsin as modified by Halmi (1952) and Dawson (1953), four types of cells can be identified in this region.

The most conspicuous cells are represented by a cell type which shall be designated as "A cells" (fig. 36). They occur in two groups situated close to the median line, and their total number of ten seems to be constant. The A cells are about 20 to 25 μ in diameter with an ovoid nucleus. The cytoplasm of these cells stains a dark purple in aldehyde fuchsin and a dark blue in chrome hematoxylin phloxin (fig. 29). They thus stand out very distinctly from the surrounding cells.

A second type of cell is found medially in the pars intercerebralis, between the two groups of A cells (fig. 36). This type consists of four cells which are of about the same size as the A cells with spherical nuclei measuring about 10 μ across. The cytoplasm of these cells appears finely granulated and stains a pale purple with the aldehyde fuchsin technique.

The third and fourth types of cells which have been observed are situated laterally in the pars intercerebralis, but some of these cells may be found more medially among the A cells. The cytoplasm of one type of these cells stains greenish with the aldehyde fuchsin technique while that of another type appears flaky, with a purplish tinge. In preparations stained in chrome hematoxylin phloxin, some of these cells show an affinity for the phloxin component of the stain. It has not been determined whether these phloxinophilic cells are identical with the cells stained green or with those stained flaky purplish after the aldehyde fuchsin method.

The constancy of the occurrence of these four types of cells in the pars intercerebralis indicates that they represent four different types of cells, although, at the present time, the possibility can not be excluded that some of them may represent different phases in the secretory cycle of a common type of neurosecretory cells.

It may be mentioned that neurosecretory cells are also found in other ganglia of the central nervous system of the milkweed bug. The first thoracic ganglion contains four such cells. The number of neurosecretory cells in the last ganglion is larger and has not been precisely determined. These cells are all rather large and stain purplish with the aldehyde fuchsin technique much like the A cells in the brain. They were not observed in the suboesophageal ganglion in *Oncopeltus*, but are found in that ganglion of the related *Lygaeus kalmii*. Such differences in the suboesophageal ganglia among related species are also reported from Hymenoptera (Thomsen, 1954).

Nayar (1955) has studied the neurosecretory cells in the nerve ring of the bug *Iphita* and has obtained somewhat different results. He did not get any selective staining by the modification of Gomori's aldehyde fuchsin which he used. He describes A cells which, like the A cells in *Oncopeltus*, appear blackish-blue after the use of chrome hematoxylin phloxin. Another type found in *Iphita* is the " B cells " which stain red with chrome hematoxylin phloxin like some of the cells in the pars intercerebralis in the milkweed bug.

The two pairs of nerves to the corpora cardiaca-allata originate from cells in the pars intercerebralis. The nervi corporis cardiaci I (fig. 36; NCC I) contain the axons of the ten A cells. They extend from the pars intercerebralis in a medioventral direction anteriorly to the central body (fig. 29). The two tracts, one on each side of the median line, cross over to the opposite side of the brain, extend in a posterior direction and leave the brain from the posterior part. The blue or purple-staining material found in the perikaryon of the A cells can be traced along the tracts inside the brain and in the cardiac nerve to the walls of the aorta (fig. 30; NM).

From the posterior part of the brain the tracts of the nervi corporis cardiaci II can be traced in a median and dorsal direction (fig. 36; NCC II). They pass very close to the medial side of the dorsal glomerulus in the mushroom bodies, do not cross the median line, and probably originate from cells in the pars intercerebralis. The axons from the four median large cells run from the pars intercerebralis caudad above the central body

and then turn ventrally. It has not been possible to determine with certainty whether these axons constitute part of the second cardiac nerves or if these nerves originate from some of the other neurosecretory cells in the pars intercerebralis.

In insects, the first cardiac nerves usually originate from two median groups of neurosecretory cells in the pars intercerebralis, while the second cardiac nerves come from two lateral groups of cells which, however, in some insects are difficult to locate. Cazal (1948) could not find the cells giving rise to the second cardiac nerves in the Hemiptera, but the fibers indicated a median position. This is also in agreement with what Pflugfelder (1936-37) found in the bug *Carpocoris*. It seems therefore that in the Hemiptera both the first and second cardiac nerves contain axons from cells in the pars intercerebralis.

From other cells in the pars intercerebralis originate the tractus chiasmaticus and, according to Pflugfelder (1936-37) and Hanström (1942a), also the ocellar stalks. The tractus chiasmaticus extends from the anterior part of the pars intercerebralis anteriorly to the central body. It is a strong fiber tract which, after crossing over to the opposite side of the brain (fig. 18c, d; TRCH), extends down to the tritocerebrum. The ocellar stalks, after reaching the brain in the dorsolateral region, can be followed as fiber tracts in a posterior and ventral direction close to the posterior border of the neuropile of the brain. The fibers pass close to the median side of the dorsal part of the mushroom body and end in the region ventral to the bridge, where also the fibers from the tractus opticus posterior end. From cells in the pars intercerebralis posterior originate a fiber tract mentioned elsewhere. It passes close to the lateral side of the bridge in an anterior direction to the border between the main and the accessory lobes and probably end in both. Some fibers from this tract seem also to be given off to the central body (fig. 21; no. 12). Impregnations with the Golgi technique did not yield good results in the pars intercerebralis.

The functional significance of the neurosecretory cells in the pars intercerebralis of adult insects has been studied by Thomsen (1952) and Dupont-Raabe (1952). Thomsen found that in the female of the fly *Calliphora* these neurosecretory cells

exert a hormonal control over the development of the ovaries. Dupont-Raabe on the other hand, observed that in phasmids the females produce eggs even if the neurosecretory cells in the pars intercerebralis have been removed. Due to their bluish-white colour, the A cells are visible in the living adult milkweed bug. In a series of experiments these cells were removed in females varying in adult age from O hour to 2 days. The surviving females developed eggs containing yolk despite the lack of A cells. It seems, therefore, that in this respect *Oncopeltus* resembles the phasmids more than the fly *Calliphora*.

The protocerebral lobes and the protocerebral commissures.— On each side, the neuropile of the protocerebrum forms two lobes. The main lobes (fig. 18c; ML) include the mushroom body, the central body and the bridge. They are laterally connected to the optic lobes. The smaller accessory lobes (fig. 18c; AL) are situated ventrad to the main lobes and dorsad to the motor center of the deutocerebrum from which they are separated by glia cells. The lobes are best developed in the anterior part. In the posterior part of the brain they are not separated from each other or from the circumoesophageal connectives.

The association cells surrounding the protocerebral lobes send their processes into the lobes, where some of them end. Fiber tracts from other parts of the brain also end here, as described previously. Silver impregnation of fibers in the lobes was often obtained, but it was impossible to determine the origin of the fibers or the connections they made.

Both the two main, and the two accessory lobes are connected by ventral commissures. Other commissural fibers surround the central body, and some are situated in the peripheral regions of the neuropile. The most distinct bundles are as follows: one uniting the two optic tubercles (fig. 21; no. 13); one in the dorsal part of the protocerebrum posterior to the one uniting the tubercles; two above the central body in the pars intercerebralis; one uniting the two halves of the bridge (fig. 21; no. 14); and some commissural fibers from the posterior optic tract (fig. 18f; TROP).

2. The Deutocerebrum

The second main part of the brain, usually called the deutocerebrum, is paired and each half consists of two parts, which have been described under several names. One part is considered a sensory center, the other a motor center.

In *Oncopeltus* the sensory centers of the deutocerebrum are well developed. They form the anterior part of the deutocerebrum, situated anteriorly on each side of the median line (figs. 17b, 18a, and 19a; DCS). They are easiy recognized in sections by their peculiar appearance; most of the neropile consists of spherical or somewhat irregular glomeruli which, together with a more loose fibrous center, give the sensory centers the appearance of a cluster of grapes. The pair of antennal nerves given off by the deutocerebrum contains, as pointed out by Titschack (1928), both motor and sensory fibers. In the milkweed bug, coarser motor fibers can be seen as a separate bundle in the dorsal part of the nerve. The sensory fibers end in the glomeruli in the sensory centers. Cells situated as a distinct group dorsolaterally in the lobes send their fibers as one large bundle into the neropile. These association neurons constitute the connections between the different glomeruli of the olfactory lobe and other parts of the brain. In all except one of the specimens examined, the fiberbundle from these cells entered the neuropile from the same direction, viz. from the dorsolateral side (fig. 18b; DCF). In the one aberrant specimen, however, the tract on one side entered the lobe from the dorsomedian direction, and the whole group of cells of the same origin had moved over to the anterior and median side. The conditions on the other side were normal.

According to Pflugfelder (1936-37), the axons of the lateral association neurons form the olfactory tract. This is a well-developed tract in *Oncopeltus*, extending from the posterior part of the olfactory lobe to the median part of the dorsal glomerulus of the mushroom bodies (fig. 21; no. 5). The olfactory lobes are connected to the central body (fig. 21; no. 11) and by a fiber tract to the motor area of the deutocerebrum. The two parts of the olfactory lobes are linked by a commissure from the posterior part of the lobes above the oesophagus (fig. 21; no. 15). None of the Golgi preparations showed good impregnation of the cells of the olfactory lobe.

The motor centers are situated posteriorly to the sensory centers and ventrally to the protocerebrum (figs. 17d, 18c, and 19b; DCM). They are not so well separated from the other parts of the brain as are the sensory centers. In the posterior part they are difficult to separate from the protocerebrum and the circumoesophageal connectives. The motor center consist of two parts. From a smaller lateral part a tract of coarse fibers runs in an anterior direction and can be seen in the ventrolateral part of the motor tract where it passes ventrally of the sensory center. Just where the antennal nerve leaves the brain, the coarse fibers cross over to the dorsal part of the tract and can be followed in the dorsal part of the nerve until the fibers leave the antennal nerve as small motor branches dorsally and laterally.

A large part of the motor center is situated more medially. The fibers from this part also extend in an anterior direction and enter the antennal nerve ventral to the olfactory lobe (fig. 19a). These fibers are, however, of about the same size as those in the sensory part of the nerve and cannot be identified as a separate bundle. The median part of the motor center, like an association body, stains darker than the surrounding parts (fig. 19b; DCM). This dark-staining region extends to the suboesophageal ganglion. The fiber tract from the sensory part of the deutocerebrum reaches mainly the median area of the motor center. From the posterior part of this center a tract runs to the ventral glomerulus of the mushroom bodies.

3. *The Tritocerebrum.*

The third part of the brain, the tritocerebrum, is much less developed than the two other parts. It is situated on each side of the oesophagus, ventrad to the motor center of the deutocerebrum and in close connection with the suboesophageal ganglion (figs. 18c and 19b; TRIT). The one pair of nerves which leaves the tritocerebrum, the labrofrontal nerves, extends from the anterior part of the tritocerebrum. The two groups of fibers of the nerve can be traced a short distance into the tritocerebrum, the labral nerve more laterally. The silver impregnations indicate that they originate in the tritocerebrum. At the point where the labrofrontal nerve leaves the brain, a commissure

combines the two parts below the pharynx (fig. 1; FRC). Besides this free commissure, the tritocerebrum of each side is connected by a strong commissure included in the same perilemma as the suboesophageal ganglion (fig. 18c; TRC). The free commissure has not been mentioned by Pflugfelder (1936-37) and probably does not occur in all bugs. Liénard (1880) has made a comparative study of this commissure and found that in the Heteroptera it is contained within the same perilemma as the suboesophageal ganglion. Malouf (1933) has observed in *Nezara* a free commissure similar to the one present in *Oncopeltus*. Whether the free commissure in the milkweed bug should be considered a frontal commissure or a tritocerebral commissure, cannot be determined before its fibers can be traced back to their origin.

Of connections to other parts of the brain the tractus chiasmaticus has been mentioned previously.

The Perilemma and the Neuroglia

Most of the information available about the non-nervous elements in the central nervous system of insects consists of short statements in papers dealing with the nervous system. Scharrer (1939) who has made a special study of these elements in the American cockroach, *Periplaneta americana*, found that the neuroglia represents a supporting tissue within the central nervous system, while the connective tissue sheath, the perilemma, covers but does not enter the nervous system. The perilemma, consists of an inner layer of cells, the perineurium, of somewhat varying thickness and appearance, and an outer non-cellular lamella, the neural lamella, which even under high power appears rather homogeneous in *Periplaneta*.

In *Oncopeltus* the perilemma consists of the usual two parts, the perineurium and the neural lamella. The perineurium forms an almost continuous layer of cells of somewhat varying appearance under the lamella (figs. 31 and 33; PN). The cells are mostly cuboidal, but in some places, e.g., in the dorsocaudal part of the brain over the mushroom bodies, and around parts of the deutocerebrum the perineurium consists of a layer of flat cells with the nuclei often far apart. In places where nerves or connectives leave the ganglia, the cells are cylindrical or irregular,

and the perineurium seems to consist of more than one layer of cells. The nuclei are small, mostly spherical or ellipsoidal, 5–6 μ in diameter, and are rich in chromatin. The stainability of the cytoplasm of the perineurium cells is not always the same. In some preparations, stained with Masson-Foot's technique, these cells stain more heavily than the neurons (fig. 31; PN), and in slides treated with Gomori's chrome hematoxylin phloxin, they show a varying affinity for the phloxin component, sometimes appearing bright red. The cell borders are mostly indistinct. As pointed out by Scharrer (1939), vitally injected trypan blue which is taken up by these cells can be used to distinguish them from the neuroglia. This is also the case in *Oncopeltus*.

The perineurium cells ensheath all the ganglia of the central nervous system, the connectives and at least the most proximal parts of the nerves. Of special interest are the conditions in the area of the pars intercerebralis where Hanström (1936, 1942a) found in *Lygaeus equestris* that the perineurium cells proliferate to form the lobus dorsomedialis. Similarly, in the same area of the pars intercerebralis of *L. kalmii* a proliferation of the perineurium cells results in a stratified epithelium. In *Oncopeltus* this condition has not been observed. However, the perineurium cells protrude somewhat into the posterior part of the brain (fig. 31; PN). In the ventral part of the last ganglion they mark the border between the second and third thoracic ganglion. In the early development of *Oncopeltus* these parts of the central nervous system are more distinctly separated than in the adult. The indentation of the adult sheath is a remnant of this situation.

The neural lamella has a varying appearance in different parts of the central nervous system. It may look like a compact sheath, 2-3 μ thick, but more often it has a fibrous structure and is split into several layers parallel to the surface of the ganglia (figs. 33 and 47a; NL). These layers are especially distinct where the larger nerves or connectives leave the ganglia. In some places the lamella connects the central nervous system and surrounding organs (fig. 32; NL) as found in other insects by Dönges (1954). Cells which occur between the layers of the

lamella, are usually quite flat, but where the lamellar layers are more separated the cells are elliptical or cuboidal. They mostly occur as single cells scattered in the lamella, but in certain areas especially in the ventral chain, they may form rows (fig. 33).

The lamella also surrounds the connectives and the larger nerves. Around the sympathetic ganglia and the corpora cardiaca-allata it is extremenly thin. The neural lamella stains blue with azan, and green with the Masson-Foot procedure, but in ordinary hematoxylin-eosin sections it is not so easily observed.

A comparison of the conditions in *Oncopeltus* and *Periplaneta* (Scharrer, 1939) shows certain differences. The lamella of the milkweed bug has a fibrous structure and is often split into layers; cells occur within these lamellar layers. These differences do not seem essential when one takes into consideration that the perilemma is a connective tissue sheath (Scharrer, l.c.). The cells which in the milkweed bug occur within the lamella are probably connective tissue cells which often cannot be differentiated from the perineurium cells proper. At times also haemocytes are observed within the neural lamella of *Oncopeltus*.

Similar conditions are reported in other insects. According to Nelson (1924), in the larva of the honey-bee the lamella is found on either side of a layer of perineurium cells. In some areas, e.g. the dorsal surface of the suboesophageal ganglion, the two components of the membrane are very close together, and the cells are flat and spaced widely apart. In the brain of certain other Hymenoptera, filaments which probably are extensions of the neural lamella are sometimes found between the perineurium cells (Thomsen, 1954). The lamella surrounding the ventral ganglia in the larva of *Oryctes nasicornis* is also split into layers which cover the layer of perineurium cells on both sides or pass back and forth through it. In these cases, the cells found within the lamella must be perineurium cells proper. On the other hand, in *Ephestia kühniella* haemocytes are, during metamorphosis, found within layers of the lamella where they seem to take part in the breakdown of the lamella in the course of the growth of the central nervous system, (Schrader, 1938).

That the neural lamella in insects is a connective tissue sheath has recently been confirmed by Meyer (1955). He observed that the lamella consists of fine elastic fibers.

When the first stage nymph of *Oncopeltus* hatches, the central nervous system is covered by a sheath of very scattered perineurium cells (fig. 35; PN). The oval nucleus is rich in chromatin. The lamella is extremely thin and difficult to observe. The development to the conditions in the adult is a gradual process. The perineurium cells multiply by mitosis and are probably diploid throughout the life of the insect. Changes in the perilemma similar to those described by Steopoe and Dornesco (1939) in *Bombyx* have not been observed.

In the central nervous system of *Oncopeltus* the glia cells are found for the most part scattered on the border between the neuropile and the groups of ganglion cells (fig. 31; GLC). They also occur around the association bodies especially those of the mushroom bodies and the central body, and sometimes between the perineurium and the neurons, among the nerve cells or within the neuropile. They are also scattered among the fibers in the connectives and the larger nerves (fig. 34).

The glia cell appears sometimes spindle-shaped, but the cell boundaries are often difficult to observe. In ordinary preparations the most conspicuous part of the gila cell is the nucleus which is usually oval in shape and quite rich in chromatin. The size of the glia cell varies. The nucleus may not be larger than that of a perineurium cell, although in *Oncopeltus* many glia cells have large, some even giant nuclei of various forms: spherical, oval, kidneyshaped, and sometimes oblong, up to 35 μ long (figs. 17a, b and 34; GLC). Gliosomes or glia fibers have not been observed with the techniques used in the present study. Vitally injected trypan blue was not taken up by any of the glia cells.

The glia cells described by Scharrer (1939) in *Periplaneta* are all small cells. Because of this difference between *Periplaneta* and *Oncopeltus* and because gliosomes and glia fibers have not been observed in the latter, the classification as glia especially of the giant cells may seem doubtful. In fact, Hanström (1936, 1942a) who has described similar giant cells in the brain of *Lygaeus equestris* and *L. kalmii* considers these cells to be peri-

neurium cells which have migrated into the brain. The nuclei of the cells in *L. equestris* seem to differ from those in *Oncopeltus* by the presence of one or more concentric structures resembling nucleoli, and by the fact that the nuclear membrane is often missing. However, the giant cells in *L. kalmii* have the same appearance as those in the milkweed bug. Besides these giant cells Hanström found ordinary small glia cells in these bugs. Pflugfelder (1952, p. 165) has observed similar giant cells in the central nervous system of *Lygaeus saxatilis*. He considers them to be tracheal end-cells. In fact, giant cells belonging to the tracheal system occur in the central nervous system of other insects, viz. in the brain of *Ephestia* (Schrader, 1938) and in the brain of the larva of the honey bee (Risler, 1954).

On the other hand, Pflugfelder (1936-37, p. 64) has described in the optic lobes of the aphid *Pemphigus bursarius* a giant cell which he considered as a glia cell. Weyer (1931) has found giant connective tissue cells in the brain of the honey bee. Recently Risler (1954) reported that in the larva of the honey bee the glia cells ("Zwischenzellen") are at first haploid (♂) or diploid, but from the 3rd larval stage they are partly tetraploid. In the brain and suboesophageal ganglion of the coleopteran *Hydrous piceus*, De Lerma (1949) has described giant cells which seem very similar to those in *Oncopeltus*. He considers them to be modified glia cells. Grandori and Carè (1951) have observed similar giant cells in the ganglia of *Musca domestica*. Thus giant cells, which probably are modified glia cells, occur in the ganglia of insects belonging to different orders.

A study of the postembryonic development of the milkweed bug has not solved the problem of the origin of the giant cells. They are already present in the first instar in the same areas as in the adult, but they are not of the same relative size (fig. 35; GLC). Cell divisions have not been observed in the giant cells, and cell counts indicate that these cells do not increase in number. The increase in size during postembryonic development is probably caused by endomitosis. The degree of polyploidy has not been determined.

The Stomodaeal Nervous System and the Corpora Cardiaca-allata.

Nabert (1913) was the first to study the stomodaeal or stomatogastric nervous system and the corpora cardiaca-allata in the Gymnocerata, although the corpora cardiaca-allata had already been described as "Ganglion cordale" by Mayer (1875) in *Pyrrhocoris apterus*. Later more information has become available through the papers by Malouf (1933), Wigglesworth (1934, 1936), Pflugfelder (1936-37), Hanström (1938, 1924b), Rawat (1939), Bickley (1942), Cazal (1948), Novák (1951), and Nayar (1953, 1954).

Cazal states that the conditions in the Gymnocerata are very uniform. The stomodaeal nervous system consists of the frontal ganglion, the recurrent nerve, the hypocerebral ganglion and an unpaired oesophageal nerve. The paired corpora cardiaca are connected with the brain by the nervi corporis cardiaci I and II which are fused nearly throughout their whole length. Depending on the species studied, the corpora cardiaca, situated below the aorta, are fused in the posterior part or along the median line. The unpaired corpus allatum, varying in size, is situated between the aorta and the oesophagus.

Bickley (1942), in a paper not mentioned in Cazal's review, has found the oesophageal nerve to be paired in *Nezara* and *Arilus*. A paired oesophageal nerve has also been found in *Pentatoma* by Hanström (1942b).

The anatomy of the stomodaeal nervous system and of the corpora cardiaca-allata in *Oncopeltus* is in agreement with the general description given by Cazal (1948) (figs. 4 and 36). The frontal ganglion (GFR) which receives fibers from the tritocerebrum, has a dorsal cellular part, whereas bundles of fibers occupy most of the ventral part (fig. 18a; GFR). The unpaired procurrent nerve extends forward (figs. 1 and 4; NP). The unpaired recurrent nerve (figs. 32 and 36; NR) passes down to the oesophagus and follows it posteriorly to the hypocerebral ganglion. In its course a few branches are given off dorsally and ventrally to the dilator muscles. According to Pflugfelder (1936-37), these branches receive their fibers from the frontal nerves. Before entering the hypocerebral ganglion the recurrent nerve

flattens and the fibers form three separate nervs (fig. 36; NR). The lateral branches run near the ventrolateral wall of the aorta and seem to enter the corpora cardiaca. A connection between the recurrent nerve and the corpora cardiaca-allata is also found in other insects (e.g., Cazal, 1948, Kaiser, 1949, Dönges, 1954). The median bundle of the recurrent nerve can be followed to the hypocerebral ganglion (fig. 36; GH). This ganglion is small and forms a flat disk between the anterior parts of the corpora cardiaca. It consists of uniform, fairly large cells (fig. 37; GH). The oesophageal nerve has so far not been identified with certainty.

The main features of the anatomy of these structures are the same in the younger stages. The hypocerebral ganglion can be more easily recognized since it is relatively larger than in the adult.

In *Oncopeltus*, the corpus allatum is unpaired, but sometimes bilobed and more or less asymmetrical, while the corpora cardiaca are paired organs as already described by Novák (1951) (figs. 4 and 36). Both corpus allatum and corpora cardiaca are intimately associated with the aorta, especially the latter which are incorporated in the ventrolateral walls of the vessel (figs. 39 and 40). The posterior parts of the corpora cardiaca are fused and closely connected with the corpus allatum (fig. 37). The fibers forming the nervi corporis cardiaci I and II can be traced back to the pars intercerebralis of the brain, as described elsewhere. In *Oncopeltus* the two nerves on each side fuse before or shortly after piercing the neural lamella of the brain. These two pairs of nerves occur in all pterygote insects (Hanström, 1940, Cazal, 1948).

In the milkweed bug there are two more connections on each side between the corpora cardiaca-allata and the central nervous system in the head. One of these is a small branch (figs. 1 and 36; NTR) which leaves the posterioventral part of the brain; shortly afterwards its fibers join the cardiac nerve. In a few cases it was found that the fibers fused with the tract of the cardiac nerve already inside the brain.

In the cicada *Dundubia* and the aphid *Pemphigus*, Pflugfelder (1936-37) has been able to show that the nerves to the copora

cardiaca-allata come from three pairs of centers in the brain. Besides two pairs in the dorsal part of the brain, a third center was observed at the basis of the tritocerebrum. In the Heteroptera examined by Pflugfelder, the tritocerebral branch was not present. Cazal (1948, p. 93) has found that in the cicada *Tettigia orni*, fibers from the tritocerebrum enter the nerves to the corpora cardiaca, thus confirming the findings of Pflugfelder. In *Oncopeltus*, it was difficult to trace the tracts of the third pair of nerves inside the ganglion. They could be followed a short distance in an anterior direction, but their origin could not be determined with certainty. It is possible that the nerve corresponds to the tritocerebral branch mentioned above as occurring in cicadas and in aphids.

Besides this connection a lateral nerve, which leaves the suboesophageal ganglion very close to the maxillary nerve, also joins the nerves to the corpora cardiaca-allata (figs. 1 and 36; NLA). Because of the great proximity of the four nerves (viz. NCC I, II, NTR, NLA) which all lie between two tracheal branches (fig. 36), it is difficult to identify the fibers of each nerve and trace them to the organs they innervate. It was, however, possible to recognize four separate fiber bundles within one neural lamella at least in some cases.

The lateral nerve (NLA) could be traced in some individuals to the dorsoposterior part of the suboesophageal ganglion. The cells from which the nerve originates, have not been found. In the Gymnocerata, Cazal (1948) has found a lateral nerve branching off from the nerves to the corpora cardiaca. Perhaps this lateral nerve is identical with the connection to the suboesophageal ganglion in *Oncopeltus*. A similar connection between the mandibular nerves and the nervi corporis cardiaci was described by Cazal (l.c.) in the Cryptocerata and are also found in other insects. It has been designated nervus corporis cardiaci collateralis (Dönges, 1954).

The nervus corporis cardiaci can be followed as a distinct structure within the dorsolateral parts of the corpora cardiaca (figs. 38 and 39; NCC). Some of the fibers seem to enter the cellular area of corpora cardiaca. Posteriorly to the corpus allatum the fibers can be followed in the walls of the aorta.

The corpora cardiaca seem to contain two types of cells (figs. 37 and 39. Large phloxinophilic cells, usually of irregular shape, are found in the two lateral halves. Smaller cells are interspersed among the larger ones, but seem to be most common in the median part. In these cells the cytoplasm is scarcely visible. Cazal (1948) considers them as glia cells.

In many insect species both the corpora cardiaca and some of the neurosecretory cells in the pars intercerebralis are easily identified in vitro by their bluish-white appearance. Correlated with this is the presence of neurosecretory material which is produced in the neurosecretory cells and transported to and probably stored in the corpora cardiaca. In the living adult of *Oncopeltus* the corpora cardiaca and some of the neurosecretory cells in the pars intercerebralis (viz., the A cells) are characterized by their bluish-white appearance. In this insect, however, the neurosecretory material produced by the A cells is evidently not stored in the corpora cardiaca but is found in the walls of the aorta (figs. 30 and 38; NM). Thus in this insect, the similarity between the corpora cardiaca and some of the neurosecretory cells in fresh appearance is not correlated with the presence of neurosecretory material in histological preparations.

The corpus allatum of *Oncopeltus* belongs to the type called "parvo-cellulaire" by Cazal (1948). It consists of many medium-sized cells of more or less the same type, and is strongly basophile, in contrast to the corpora cardiaca. The histological picture varies with the age of the animal.

In the newly emerged adult the cells form a compact body, and the cell borders are difficult to observe. During the adult stage the size of the corpus allatum increases considerably in the females and somewhat less in the males as described by Novák (1951). This growth is so pronounced that it is easily noticed in dissections. During the later period of life there seems to be a decrease in size. The increase after emergence, is accomplished during the first period of adult life by an increase in cell number (fig. 38; CA), but later also by an increase in cellular and nuclear size. In the corpus allatum of an old female we thus find, besides the small nuclei, large nuclei of irregular shape (fig. 40). Intercellular spaces are also frequent in old adults. Nayar

(1953) has found in the bug *Iphita* that the secretory products of the corpus allatum stain a dark blue in Gomori's chrome hematoxylin phloxin. Similar observations have not been made during the present study in *Oncopeltus*.

Variation in the size of the corpus allatum according to age have been noticed by a number of investigators among them Nabert (1913) in his study of *Pyrrhocoris*. Nayar (1953) has found that in females of *Iphita* the maximal size of corpus allatum is reached when the animal develops eggs. A sexual difference in the size of corpus allatum is also reported for several insects as discussed by Palm (1949).

As in other groups of insects, the endocrine role of the corpus allatum in adult Hemiptera concerns reproductive processes. As in *Rhodnius* (Wigglesworth, 1936), this gland controls the formation of ripe eggs in *Oncopeltus*. Thus in specimens where the head and prothorax have been removed the oocytes do not grow beyond a certain stage and no yolk is deposited. Implantation of corpora allata taken from mature donors will result in the formation of ripe eggs in such ligated females.

The Postembryonic Growth and Development of the Central Nervous System.

The central nervous system of the milkweed bug is much more concentrated in the first instar than in the adult (fig. 44). At this stage the two halves of the protocerebrum are dorsally separated by a narrow slit, which in the anterior part widens to give space to the dilator muscles of the pharynx. Posteriorly the fissure nearly reaches the central body (fig. 41b). The optic lobes are easily distinguished from the rest of the brain, but they are much less developed than in the adult. They are relatively thin, flattened dorsoventrally, and they are curved ventrally. The convex side follows the outline of the head. The optic nerves are thin and distinctly separated from the broader lobes. They leave from the distal point of the lobes (fig. 41a; NO). The ocelli are undeveloped, and no ocellar stalks are present. The deutocerebrum is less differentiated than in the adult, although the antennal nerves are the strongest nerves to the brain. Ex-

ternally the tritocerebrum is not clearly marked off. The suboesophageal ganglion is very closely connected with the brain (fig. 41b) and is situated farther forward—i.e. right under the brain—than in the adult.

The rest of the ganglia are all elliptical in shape, the long axis running in the lateral direction. The first thoracic ganglion is situated in the prothorax, the other ventral ganglia are concentrated in the meso- and metathorax. In the first instar it is possible externally to identify the second and third thoracic ganglia from the abdominal ones, which here, as in the adult are united in a single mass.

The separation of the central nervous system into a peripheral cellular cortex and a central neuropile takes place during the embryological period (Butt, 1949). In the first instar the ganglion cells are only slightly differentiated into different morphological types, such as globuli cells, ordinary association cells, and larger motor cells. In the neuropile of the brain all the association bodies which occur in the adult are present (figs. 41 and 42). The mushroom bodies and the central body consist of the same parts as in the adult, and in the medulla externa the three main layers can be observed. The Golgi impregnations gave less satisfactory results than in the adult, but some of the associative cell types found in the adult were also observed in the first instar (fig. 43).

During postembryonic development the growth rate of the body as a whole surpasses that of the central nervous system. Consequently, in the adult the mass of the central nervous system represents a smaller proportion of the total body mass than in the first instar (figs. 45 and 46. While the central nervous system makes up about 10% of the total body volume in the first instar, this value decreases to about 2% in the third instar and to 0.3% in the adult male. In this process of gradual growth and development the connectives become longer and the ganglia more separated (fig. 44). Furthermore, the ganglia of the third thoracic and abdominal segments become more and more displaced from their proper segments.

During the growth of the central nervous system, also the relative size of the different ganglia changes somewhat as shown in

table 1. There is a decrease in the relative mass of the brain and suboesophageal ganglion, while that of the thoracic and abdominal ganglia increases. By contrast, Cody and Gray (1938) have found that in the coleopteran *Passalus cornutus* the brain and suboesophageal ganglion retain their proportional size in relation to other ganglia during development.

During this process of growth the neuropile areas increase more in size than the cortex. This happens both in the brain and in the first thoracic ganglion which have been chosen as examples (table 2).

The volume of the different bodies in the brain has also been measured and compared with the volume of the total brain and the volume of the undifferentiated neuropile areas of the brain in question (table 3). The primary centers, such as the olfactory lobe and the three optic bodies, occupy a much greater part of the brain in the adult than in the first instar. On the other hand, the relative size of the central association centers changes only slightly. That of the central body and the bridge decreases while that of the mushroom bodies increases slightly. The changes in relative size of the centers must be the result of different rates of growth. Table 4 shows that the greatest increase in actual size takes place in the lamina ganglionaris, and that

Table 1: Volume of ganglia and connectives in % of total central nervous system

Instars	Brain	Sub. gn.	I th. gn.	Last gn.	Connectives
1st	59	16	8	17	<1
3rd	50	16	9	25	<1
Ad. ♂	48	12	10	27	3

Table 2: Volume of cortex and neuropile in % of total volume of ganglia

	Brain		I. thoracic gangl.	
Instars	Cortex	Neuropile	Cortex	Neuropile
1st	70	30	67	33
3rd	61	39	52	48
Ad. ♂	47	53	33	67

Table 3: Volume of association bodies in % of total brain and undifferentiated neuropile.

Instars	Lamina gangl.		Medulla externa		Medulla interna		Olfact. lobe		Mushr. bodies		Central body		Bridge	
	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.	Total brain	Undiff. neurop.
1st	0.6	3	1.7	8	0.9	4	2.2	11	2.6	11	0.8	4	0.2	1.0
3rd	1.6	7	3.7	16	1.3	6	4.6	20	2.9	12	0.8	3	0.1	0.5
Ad. ♂ ..	3.2	13	6.9	29	2.4	10	10.9	45	3.1	12	0.6	3	0.1	0.3

Table 4: Absolute increase in volume of association bodies from first to adult stage

Lamina gangl.	Medulla externa	Medulla interna	Olfact. lobe	Mushr. bodies	Central body	Bridge
56 ×	41 ×	29 ×	45 ×	12 ×	7 ×	5 ×

the increase of the optic bodies is less pronounced in their proximal direction. The difference in growth rate between the primary sensory centers and the central association centers is evident.

The data given on the growth of the central nervous system of *Oncopeltus* must be treated with caution. A comparison with data collected in other insects is difficult because of variations in methods used and difficulties in determining the border between the brain and the circumoesophageal connectives.

The growth of the central nervous system is in part accomplished by cellular multiplication. In the first instar nymph certain areas of the central nervous system are characterized by mitotic activity. For example, in the posterior part of the brain there are two neuroblasts on each side just below the perilemma which are easily recognized by their large size (fig. 18f; NBL; fig. 47). By unequal division they produce daughter cells ("Ganglienmutterzellen" of Bauer, 1903) which are small cells with dark staining nuclei (fig. 47a, b, c). In sections the daughter cells are found in close proximity to the neuroblasts. By equal division the daughter cells produce two neurons (fig. 47d). These divisions are only rarely observed, but they have been found in both instars and adult specimens. This could mean that daughter cells can differentiate directly into neurons. During the embryological period in *Oncopletus* the ganglion cells are differentiated directly from the daughter cells (Butt, 1949). This is also the case in the embryoes of the grasshopper *Chortophaga* which has been much used in the study of nerve cell formation (Roberts, 1955). In *Ephestia* on the other hand, during postembryonic development nerve cells are differentiated both directly from the daughter cells and from cells obtained by an equal division of the daughter cells (Schrader, 1938). The latter type of nerve cell formation has been found in the larva of the honey bee (Risler, 1954).

Besides the four neuroblasts in the posterior part of the brain, at least one similar neuroblast is found on each side dorsally in the olfactory lobe on the border to the optic lobes (fig. 47d). Here the formation of neurons seems to take place in the same way.

The most intensive mitotic activity takes place in the optic lobes. The optic bodies are surrounded by two areas of smaller neuroblasts, but the way in which the neurons are formed here, has not been studied in detail.

The neuroblasts in the posterior part of the brain and those dorsally in the olfactory lobes do not degenerate as soon as the imaginal stage is reached, but are present during the first part of adult life. Cell divisions have frequently been observed in adults (fig. 47a, c), even in specimens which were one month adult age. This indicates that the brain of *Oncopeltus* is capable of growing in the imago. It does not, however, exclude that the number of nerve cells may decrease during adult life as has been observed in the honey bee (Rockstein, 1950).

Except for a few cell divisions which may be observed in the first instar, no multiplication of nerve cells and no neuroblasts have been observed in the suboesophageal and first thoracic ganglia during the postembryonic development. There is, however, an increase in the size of these ganglia. In the first thoracic ganglion, which has been chosen as an example, the growth is accomplished by an increase in the volume of both cortex (6 fold) and neuropile (24 fold). These measurements refer to the period between the first instar and the adult age. Since the increase in the volume of the cortex of the first thoracic ganglion is not based on cellular multiplication, it must be accounted for by an increase in the nuclear size and/or the internuclear distances. A similar mode of growth of the ventral chain has been observed by Grosch (1950) in *Habrobracon*. No mitotic activity was found here either, the growth being accomplished by an increase in internuclear distances during the first larval stage and later by an increase in the mass of the neuropile. In *Locusta migratoria,* Roonwal (1937) has observed that the neuroblasts degenerate during the embryonic period. Trager (1937), on the other hand, has found that the thoracic ganglia of *Aedes aegypti* grow during the larval stages by cellular multiplication.

The main increase in the volume of the ganglia of *Oncopeltus* is caused by an increase in the neuropile (table 2). It seems to be a general pattern that the neuropile occupies a relatively smaller part in the central nervous system of immature forms than in adult insects. In *Drosophila*, Power (1952) has observed an increase in the neuropile from about 18% of the total volume of the central nervous system to about 53%. Here the neuropile was found to increase in mass even after the nervous system as a whole had ceased to grow.

Most cases in which the central nervous system of immature forms has been previously studied refer to hemi- or holometabolous insects where larvae and adults are morphologically and/or biologically rather different. Even in these cases the central association bodies and main fiber tracts are often already present in larval forms (e.g. Baldus, 1924, Beier, 1927, Rogoff, 1943). In some cases the central body has not been observed, viz. in the young larvae of Lepidoptera (Hanström, 1925) and Coleoptera (Murray and Tiegs, 1935). Hanström (l.c.) mentions also that the bridge does not appear in the brain of the newly hatched larva of the cabbage butterfly, and that the brain as a whole is much more primitive than that of the adult. The degree of development of the central nervous system must be correlated with alterations in the behavior pattern during development. In *Oncopeltus* where this pattern changes but little it is not surprising to find the same main structural features in the brain of both immature and adult forms. It would be interesting to see whether in this case the growth is only quantitative, (an increase in size and number of cell types and fiber tracts already present), or if new types of cells of fiber tracts develop during the postembryonic period. A more thorough quantitative study of the growth of the different parts is needed for a comparison with results found in holometabolous insects by Power (1952).

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Summary.

1. The central nervous system of the milkweed bug consists of four ganglia: the brain, the suboesophageal ganglion, the first thoracic ganglion, and one composite ganglion containing the second and third thoracic ganglia plus all the abdominal ganglia. The main features of the anatomy of the nervous system are described.

2. The histology, the pattern of fiber tracts, and the types of neurons in the brain are similar to those described from Gymnocerata by Pflugfelder (1936-37).

3. After the use of Gomori's aldehyde fuchsin technique four types of neurosecretory cells can be identified in the pars intercerebralis region of the brain. From one type of these cells (the A cells) neurosecretory material can be traced along the nervus corporis cardiaci I to the walls of the aorta.

4. Owing to their bluish-white colour the ten A cells are visible in the living adult milkweed bug. Removal of these cells from newly emerged females did not prevent the development of eggs.

5. The central nervous system is covered by the perilemma, which consists of a neural lamella and a layer of perineurium cells. The fibrous lamella may contain cells which are considered as perineurium cells, connective tissue cells, and haemocytes.

6. Besides ordinary small glia cells, giant cells which are supposed to be modified glia cells are found within the central nervous system.

7. The corpora cardiaca-allata have three pairs of nervous connections with the brain: the mostly fused nervi corporis cardiaci I and II, and a nerve which probably originates in the

tritocerebrum. Connections with the suboesophageal ganglion and the recurrent nerve are also present.

8. All association bodies found in the brain of the adult are already present in the first instar.

9. In the adult the mass of the central nervous system represents a smaller proportion of the total body mass than in the first instar.

10. During postembryonic development there is a decrease in the relative mass of the brain and the suboesophageal ganglion while that of the thoracic and abdominal ganglia increases.

11. During this process of growth the neuropile areas increase more in size than the cellular cortex.

12. The increase in size of the sensory centers (optic bodies and olfactory lobes) is greater than that of the central association bodies in the brain. Among the optic bodies, lamina ganglionaris shows the greatest increase, medulla interna the smallest.

13. In the posterior part of the brain two pairs of neuroblasts produce daughter cells by unequal divisions. Neurons are formed by equal division of the daughter cells, and perhaps also directly from the daughter cells. Divisions of the neuroblasts were also observed in the imago. No neuroblasts were found in the suboesophageal and the first thoracic ganglia.

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Abbreviations.

AD_1: first adductor of the labium
AL: accessory protocerebral lobe
ANTM: antennal muscle
AO: aorta
BR: bridge
BRN: brain
CA: corpus allatum
CB: central body
CBD: central body, dorsal part
CBT: central body, tubercle
CBV: central body, ventral part
CC: corpora cardiaca
CHE: chiasma externum
CPD: corpus pedunculatum, dorsal glomerulus
CPR: corpus pedunculatum, roots
CPRP: corpus pedunculatum, ramus posterior
CPRS: corpus pedunculatum, ramus superior
CPS: corpus pedunculatum, stalk
CPV: corpus pedunculatum, ventral glomerulus
D_1: dorsal muscle of first abdominal segment
DCF: fibers entering deutocerebrum
DCM: deutocerebrum, motor part
DCS: deutocerebrum, sensory part
DLBC: dilator of buccales
DLCB: dilator of cibarium
DLPHY: dilator of pharynx
DLSYR: dilator of syringe
EF: erection fluid reservoir
FRC: frontal commissure
FU_{1-3}: furca of the first-third thoracic segment
GFR: frontal ganglion

GH: hypocerebral ganglion
GLC: glia cell
LG: lamina ganglionaris
LGC: lamina ganglionaris, cellular layers
LGN: last ganglion
LMPHY: longitudinal muscle of pharynx
LO: optic lobe
LVR: lever
MD: mandible
MDH: hypopharyngeal-mandibular muscle
MDPR: mandibular process
ME: medulla externa
MI: medulla interna
ML: main protocerebral lobe
MS: mesadenes
MX: maxilla
NAB_{1-7}: first-seventh abdominal nerve
NANT: antennal nerve
NBL: neuroblast
NCC I, II: nervus corporis cardiaci I, II
NL: neural lamella
NLA: lateral nerve
NLB: labial nerve
NLBR: labral nerve
NM: neurosecretory material
$NMAT_{1-2}$: first-second metathoriacic nerve
NMD: mandibular nerve
NMT_{1-4}: first-fourth mesothoracic nerve
NMX_{1-2}: first-second maxillary nerve
NO: optic nerve
NP: procurrent nerve
NPT_{1-4}: first-fourth prothoracic nerve
NR: recurrent nerve
NSG: salivary gland nerve
NTR: tritocerebral nerve
OE: oesophagus
OS: ocellar stalk
PHR_2: second phragma
PI: pars intercerebralis
PMX: protractor of maxilla
PN: perineurium
RE: rectum
RMD: retractor of mandible
RMX: retractor of maxilla
SGN: suboesophageal ganglion
SV: seminal vesicle

TE: testis
TO: tuberculum opticum
TR: trachea
TRC: tritocerebral commissure
TRCH: tractus chiasmaticus
TRIT: tritocerebrum
TROA: tractus opticus anterior
TROMI: tractus opticus medialis inferior
TROMS: tractus opticus medialis superior
TROP: tractus opticus posterior
V_{1-5}: ventral muscle of first-fifth abdominal segment
I-III THGN: first-third thoracic ganglion

Numbers on muscles in figs. 2-14 refer to Larsén (1945).

1: Musculus pronoti primus
2: M. pronoti secundus
3: M. pronoti tertius
4: M. pronoti quartus
5: M. pronoti quintus
6: M. prosterni primus
7: M. prosterni secundus
9: M. dorsoventralis
10: M. proepisterno-postoccipitalis
13: M. noto-trochantinalis
14: M. noto-coxalis primus
16: M. noto-coxalis tertius
17: M. pleura-coxalis
20: M. noto-trochanteralis
21: M. pleura-trochanteralis
22: M. furca-trochanteralis
30: M. mesonoti primus
31: M. mesonoti secundus
32: M. mesosterni primus
34: M. dorsoventralis primus
35: M. dorsoventralis secundus
39: M. furca-pleuralis
40: M. noto-trochantinalis
41: M. noto-coxalis
42: M. episterno-coxalis
43: M. coxa-subalaris
46: M. noto-trochanteralis
47: M. pleura-trochanteralis
57: M. metanoti secundus
58: M. metasterni primus
60: M. dorsoventralis
63: M. noto-trochantinalis

64: M. noto-coxalis
65: M. episterno-trochantinalis
66: M. episterno-coxalis
67: M. coxa-subalaris
69: M. furca-coxalis posterior
70: M. noto-trochanteralis
71: M. pleura-trochanteralis
72: M. furca-trochanteralis

Numbers on figs. 21 and 22 refer to fiber tracts and cell types described in the text.

Explanation of Figures.

Figure 1: Head. Approximately median section. Adult specimen. Side view.

Figure 2: Head. Section more lateral than the one shown in figure 1. Adult specimen. Side view.

Figure 3: Head. Section more lateral than the one shown in figure 2. Adult specimen. Side view.

Figure 4: Half of the head. Adult specimen. Dorsal view.

Figure 5: Half of the head. Section more ventral than the one shown in figure 4. Adult specimen. Dorsal view.

Figure 6: Half of the head. Section more ventral than the one shown in figure 5. Adult specimen. Dorsal view.

Figure 7: Prothorax. Approximately median section. Adult specimen. Side view.

Figure 8: Prothorax. Section more lateral than the one shown in figure 7. Adult specimen. Side view.

Figure 9: Prothorax. Section more lateral than the one shown in figure 8. Adult specimen. Side view.

Figure 10: Mesothorax. Approximately median section. Adult specimen. Side view.

Figure 11: Mesothorax. Section more lateral than the one shown in figure 10. Adult specimen. Side view.

Figure 12: Mesothorax. Section more lateral than the one shown in figure 11. Adult specimen. Side view.

Figure 13: Metathorax. Approximately median section. Adult specimen. Side view.

Figure 14: Metathorax. Section more lateral than the one shown in figure 13. Adult specimen. Side view.

Figure 15: Abdomen and part of thorax. Right genital organs removed. Old adult male. Dorsal view.

Figure 16: Schematic drawing showing the nerves of the last ganglion. Adult specimen.

Figure 17a-d: Brain. Adult specimen. Frontal sections. Alcoholic Bouin, Masson Foot. 10 μ.

Figure 18a-f: Brain and suboesophageal ganglion. Adult specimen. Transverse sections. Alcoholic Bouin, Masson Foot. 10 μ.

Figure 19a-c: Brain and suboesophageal ganglion. Adult specimen. Sagittal sections. Alcoholic Bouin, Masson Foot. 10 μ.

Figure 20a-c: Optic nerve. Adult specimen. Cross sections. Anterior direction to the right. a: near the compound eye. b: through the outer cellular layers of lamina ganglionaris. c: through the endings of the retinal fibers in lamina ganglionaris. Alcoholic Bouin, Heidenhain's ironhematoxylin. 7 μ.

Figure 21: Schematic reconstruction of the brain showing the main fiber tracts. Adult specimen. Dorsal view.

Figure 22: Schematic drawing of the nuerons in the optic lobe. White neurons were not impregnated. Adult specimen. Golgi method. Modified from Pflugfelder (1936-37).

Figure 23: Impregnation of the dorsal and ventral glomerulus of corpus pedunculatum. Adult specimen. Golgi method.

Figure 24: Impregnation of collaterals to the ventral glomerulus of corpus pedunculatum. Adult specimen. Golgi method.

Figure 25: Schematic drawing of impregnations in the central body. Adult specimen. Golgi method.

Figure 26: Impregnation of the dorsal part of the central body. Adult specimen. Sagittal section. Golgi method.

Figure 27: Impregnation of the ventral part of the central body. Adult specimen. Horizontal section. Golgi method.

Figure 28: Impregnation of the bridge. Adult specimen. Golgi method.

Figure 29: Brain. Median section showing neurosecretory cells in the pars intercerebralis. Adult specimen. Aqueous Bouin, Gomori's chrome-hematoxylin-phloxin. 7 μ.

Figure 30: Aorta with neurosecretory material. Adult specimen. Transverse section. Helly, Gomori's aldehyde fuchsin. 7 μ.

Figure 31: Posterior part of the brain. Adult specimen. Horizontal section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 32: Posterior part of the brain showing intimate connection between aorta and neural lamella. Fourth instar. Sagittal section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 33: Dorsal part of the last ganglion. Fifth instar. Sagittal section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 34: Connective between first thoracic and last ganglion. Fifth instar. Sagittal section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 35: Ventral part of the suboesophageal ganglion. First instar. Transverse section. Alcoholic Bouin, Masson Foot. 5 μ.

Figure 36: Semi-schematic drawing showing connections between the corpora cardiaca-allata, the brain, and the stomodaeal nervous system. Adult specimen. Dorsal view.

Figure 37: Ganglion hypocerebrale and corpora cardiaca. Adult specimen. Horizontal section. Masson Foot. 7 μ.

Figure 38: Corpora cardiaca-allata. Young adult female. Sagittal section. Aqueous Bouin, Gomori's chrome-hematoxylin-phloxin. 7 μ.

Figure 39: Aorta and corpora cardiaca. Adult female. Transverse section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 40: Corpus allatum. Old adult female. Transverse section. Alcoholic Bouin, Masson Foot. 7 μ.

Figure 41a-c: Head with brain and suboesophageal ganglion. First instar. Transverse sections. Helly, Masson Foot. 10 μ.

Figure 42: Head and thorax with the central nervous system. First instar. Sagittal section. Helly, Masson Foot. 10 μ.

Figure 43: Impregnation of corpus pedunculatum. First instar. Golgi method.

Figure 44: Central nervous system of the various instars. Dorsal view.

Figure 45a-b: Outlines of first instar with central nervous system. a: dorsal view. b: lateral view.

Figure 46a-b: Outlines of adult male with central nervous system. a: dorsal view. b: lateral view.

Figure 47a-d: Neuron formation in the brain. a-c: posterior part of the brain, d: olfactory lobe. a: Neuroblast in metaphase. Adult specimen. Aqueous Bouin, Masson Foot. 7 μ. b: Neuroblast in anaphase. First instar. Carnoy, Heidenhain's ironhematoxylin. 5 μ. c: Neuroblast in telophase. Adult specimen. Alcoholic Bouin, Masson Foot. 10 μ. d: Daughter cell in telophase. First instar. Alcoholic Bouin, Masson Foot. 5 μ.

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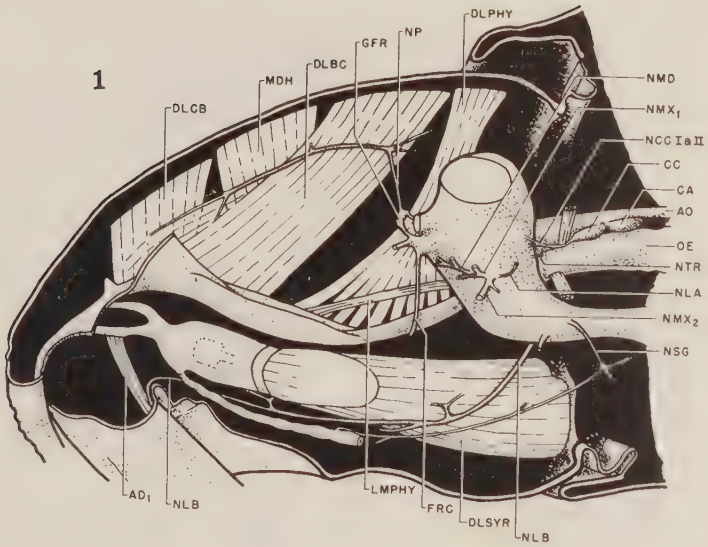
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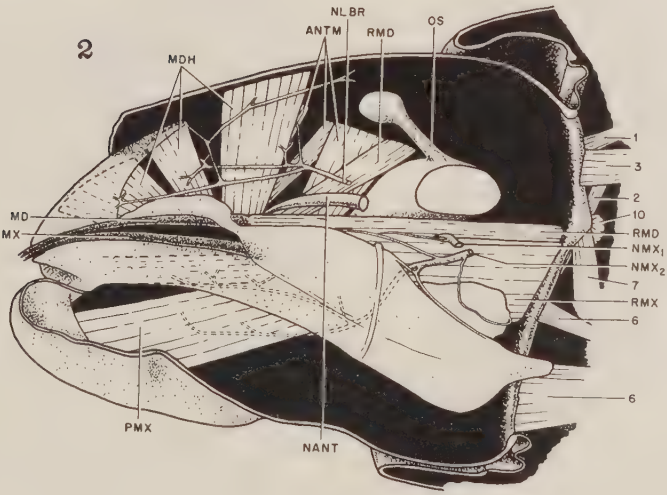
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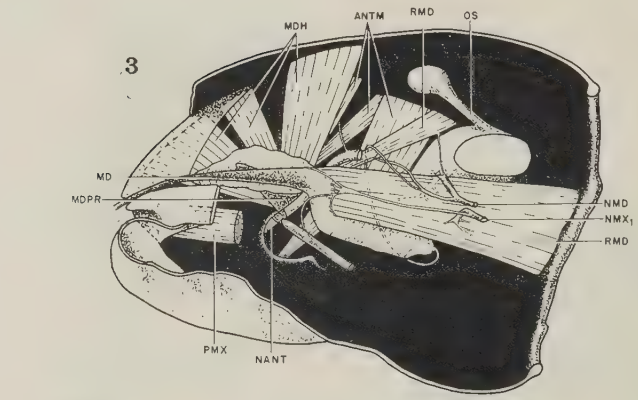
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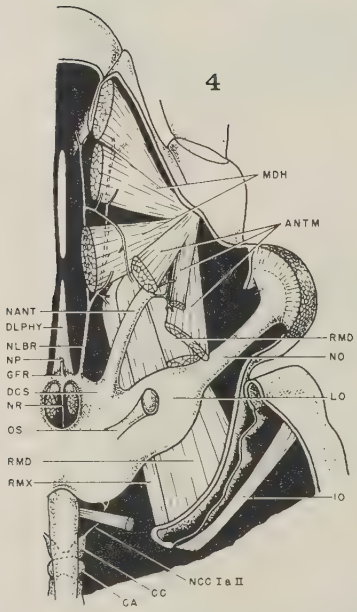
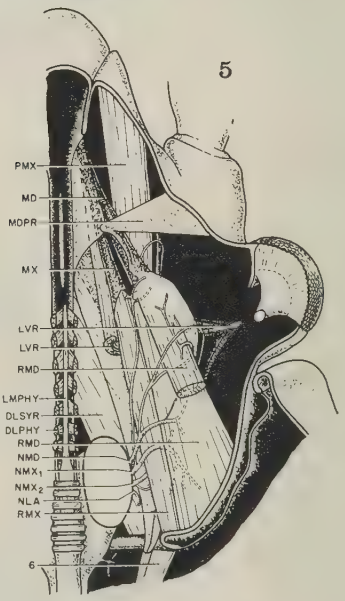
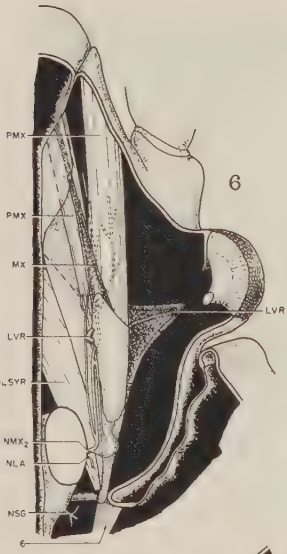
MDH
ANTM
RMD
OS
MD
MDPR
NMD
NMX1
RMD
PMX
NANT


4
MDH
ANTM
NANT
DLPHY
NLBR
NP
GFR
DCS
NR
OS
RMD
RMX
RMD
NO
LO
IO
NCC I & II
CC
CA


5
PMX
MD
MDPR
MX
LVR
LVR
RMD
LMPHY
DLSYR
DLPHY
RMD
NMD
NMX1
NMX2
NLA
RMX
6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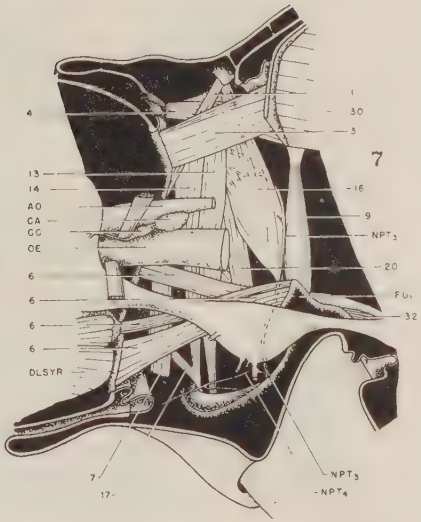
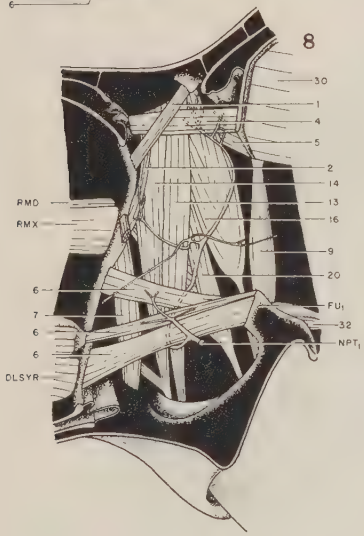
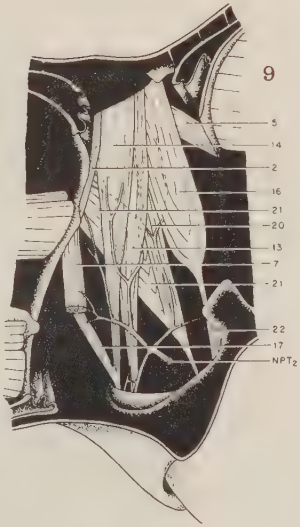
PMX
PMX
MX
LVR
LVR
DLSYR
NMX2
NLA
NSG
6


7
4
13
14
AO
CA
CC
OE
6
6
6
6
DLSYR
1
30
3
16
9
NPT3
20
FU1
32
7
17
NPT3
NPT4


8
30
1
4
5
2
14
13
16
9
20
FU1
32
NPT1
RMD
RMX
6
7
6
6
DLSYR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5
14
2
16
21
20
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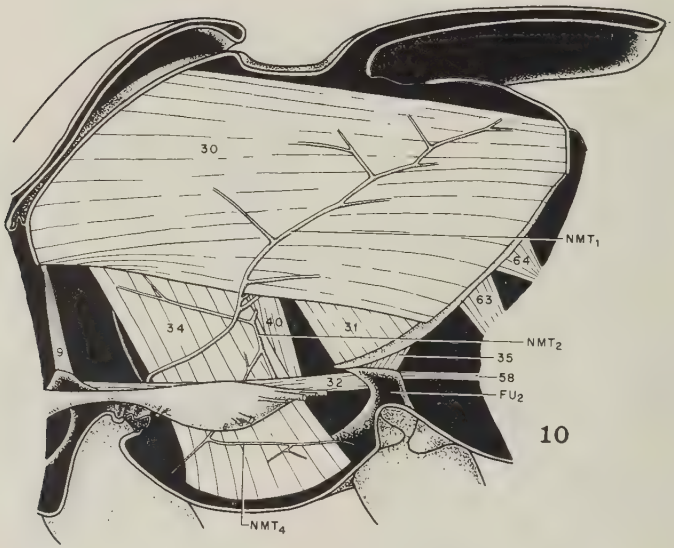
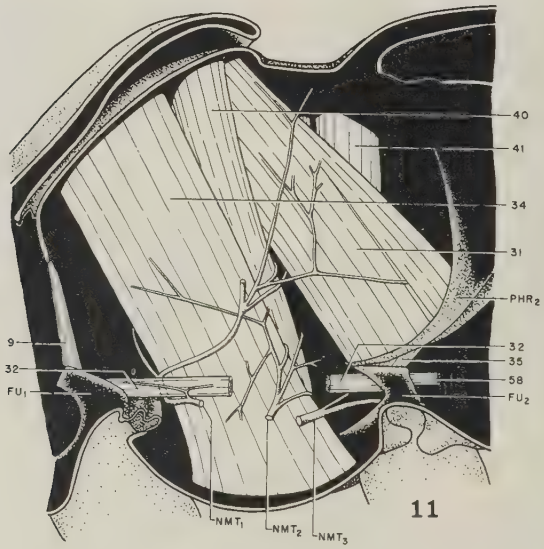
7
21
22
17
NPT2


30
NMT1
64
63
34
40
31
NMT2
9
35
58
32
FU2
NMT4

10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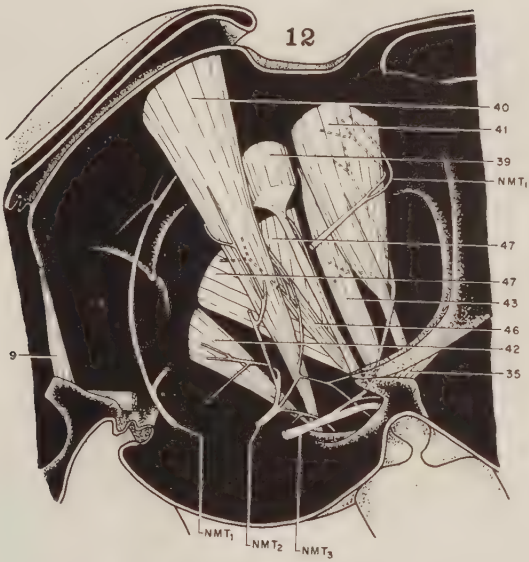
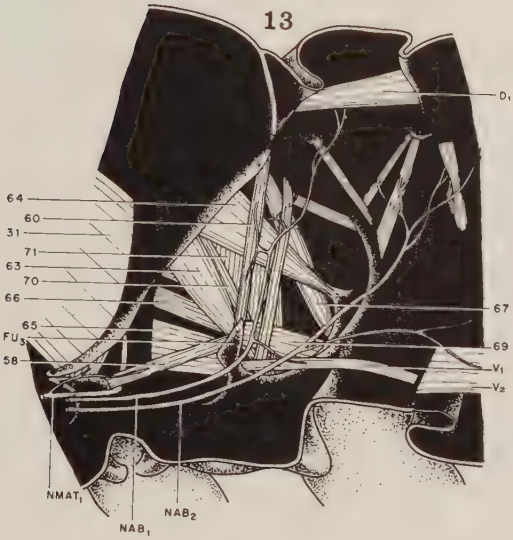
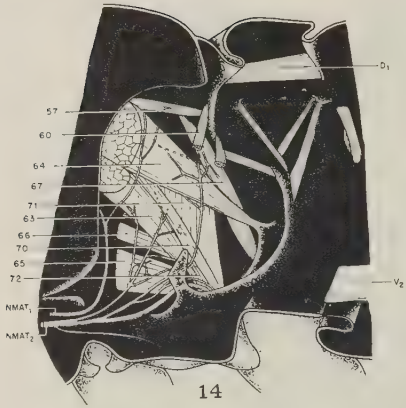
PHR2
9
32
32
35
FU1
58
FU2
NMT1
NMT2
NMT3

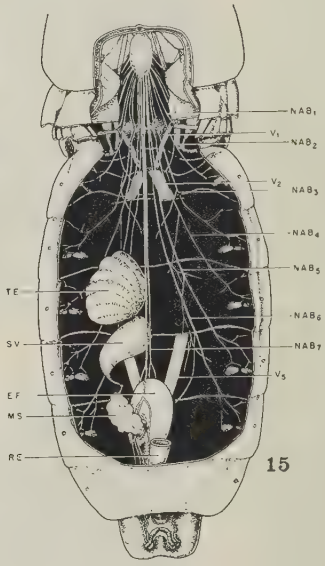
11


12
40
41
39
NMT1
47
47
43
46
42
35
9
NMT1
NMT2
NMT3

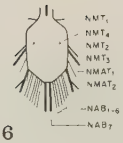

13
D1
64
60
31
71
63
70
66
65
FU3
58
67
69
V1
V2
NMAT1
NAB1
NAB2


D1
57
60
64
67
71
63
66
70
65
72
NMAT1
NMAT2
V2

14

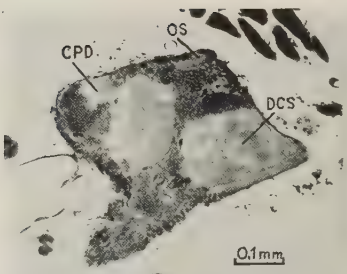

NAB1
V1
NAB2
V2
NAB3
NAB4
NAB5
TE
NAB6
SV
NAB7
V3
EF
MS
RC

15

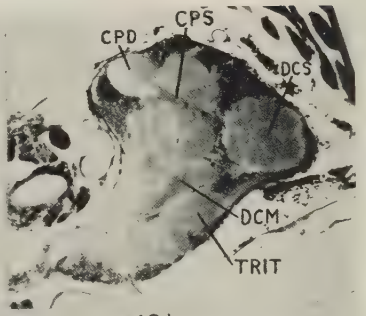

NMT1
NMT4
NMT2
NMT3
NMAT1
NMAT2
NAB1-6
NAB7

16

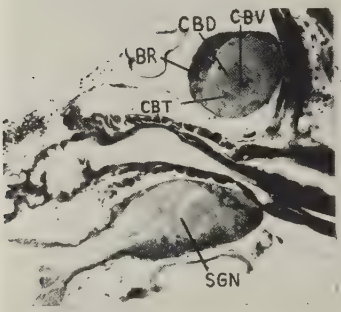
TROA
GLC
ME
MI
CPD
PI
0.1 mm.
17 a
LGC
DCS
GFR
LG
GLC
ME
MI
CPS
CPR
CPV
CB
CPD
17 b
DCS
GLC
LGC
17 c
CPR
BR
DCM
17 d
NP
CHE
ME
DCS
GFR
18 a
LG
0.1 mm.
ME
OS
18 b
DCF
MI
AL
ML
18 c
CPR
DCM
TRCH
MI
TRC
TRCH
CPRS
CPS
CPRP
18 d
DCM
TRIT
CPD
CPS
CPR
18 e
SGN
BR
CPD
NBL
TROP
18 f



19 a

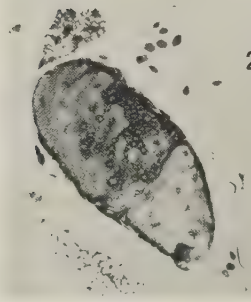


19 b

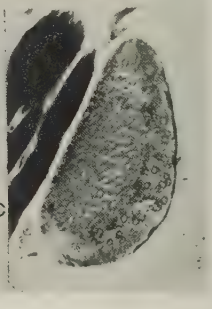


19 c

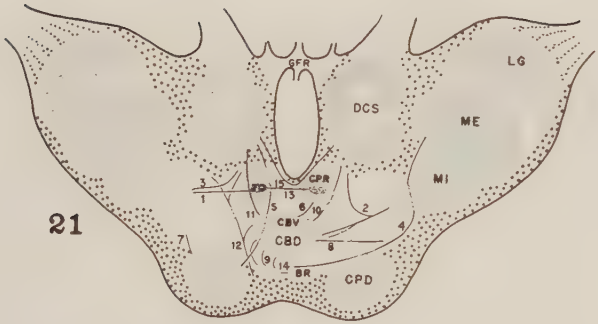
20 a

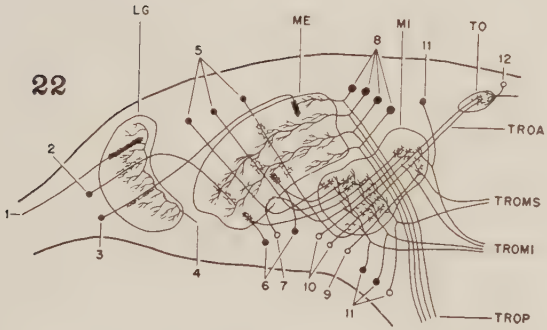


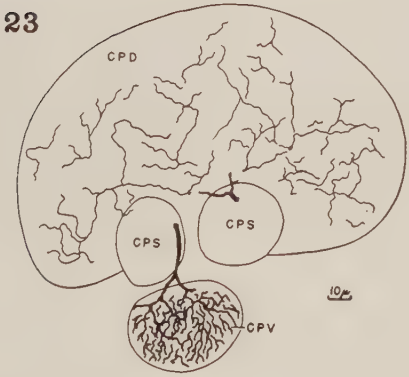
20 b



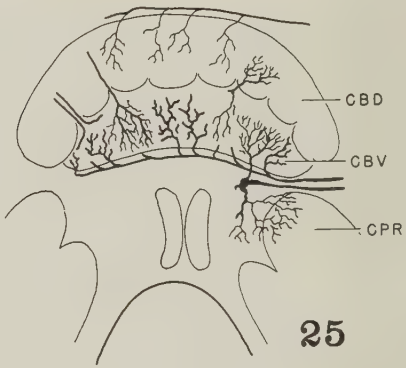
20 c


21
GFR
LG
DCS
ME
MI
CPR
CBV
CBD
BR
CPD


22
LG
ME
MI
TO
TROA
TROMS
TROMI
TROP


23
CPD
CPS
CPS
CPV
10μ

24



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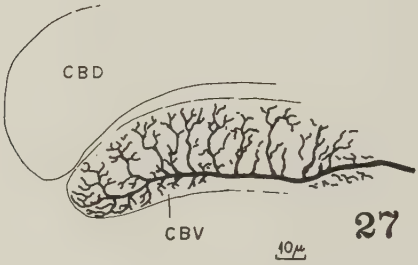

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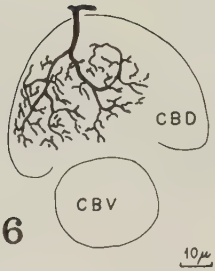

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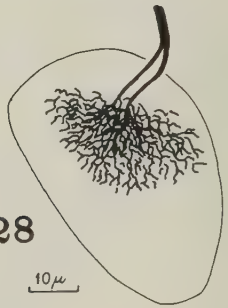

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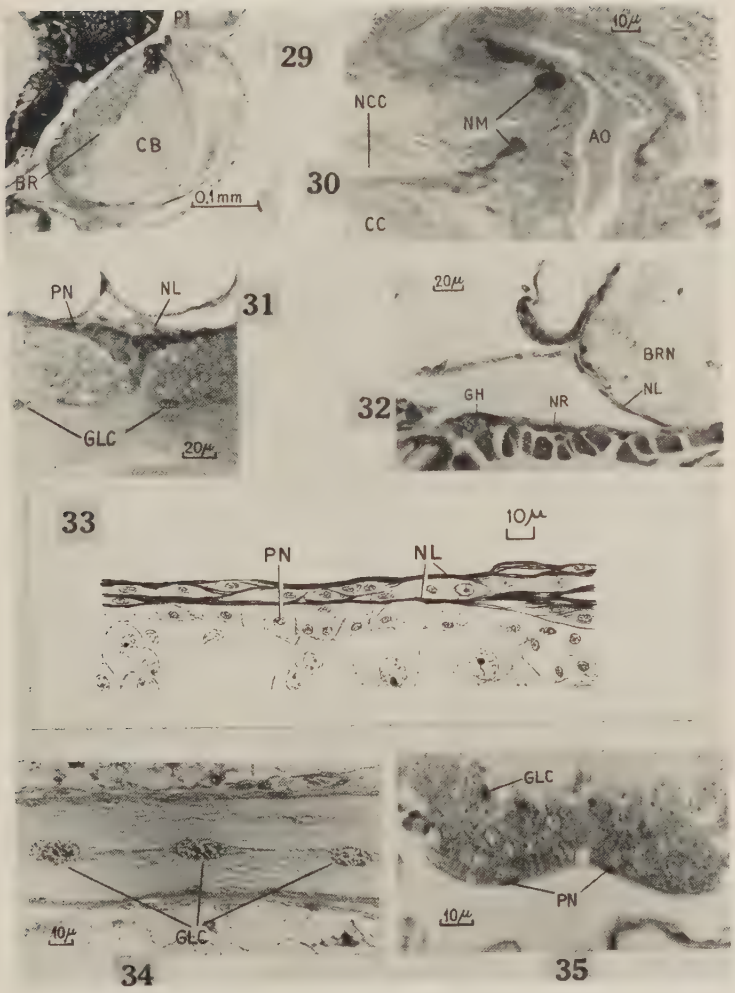
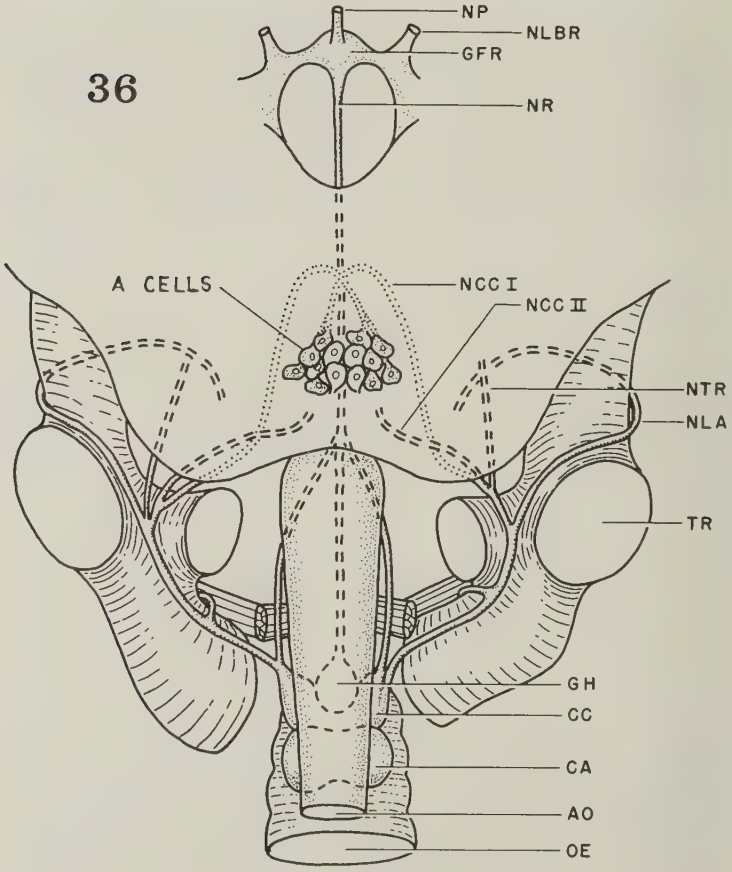
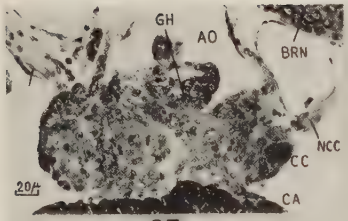

29
PI
CB
BR
0.1 mm
30
10μ
NCC
NM
AO
CC
31
PN
NL
GLC
20μ
32
20μ
BRN
NL
GH
NR
33
10μ
PN
NL
34
10μ
GLC
35
GLC
PN
10μ

36





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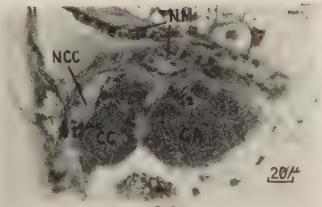

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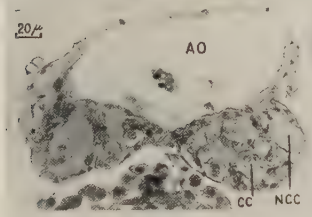

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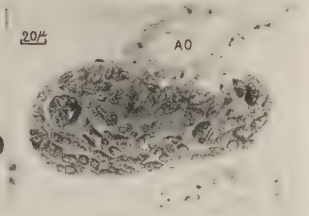

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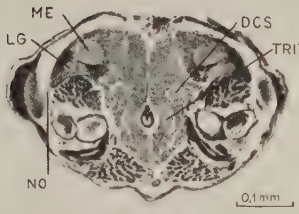
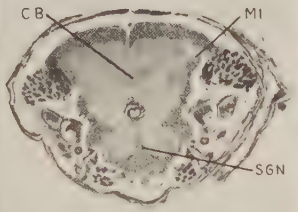
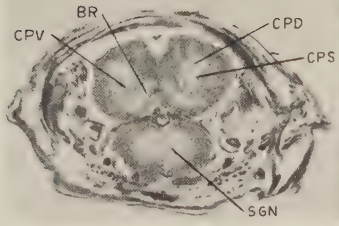


41a



41b

41c



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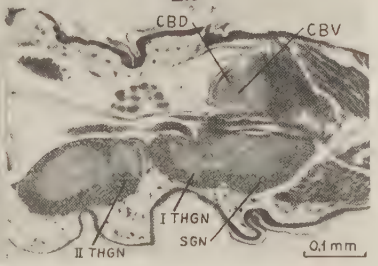

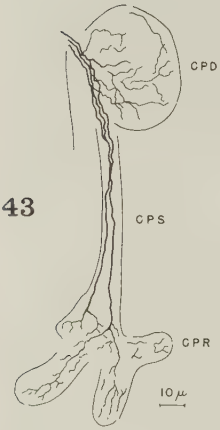

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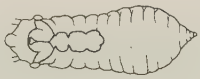
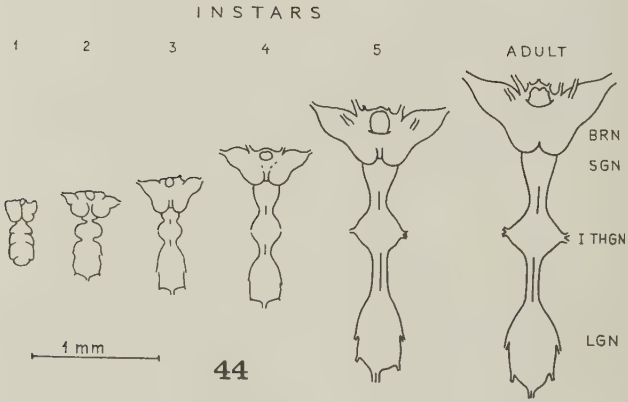


45a

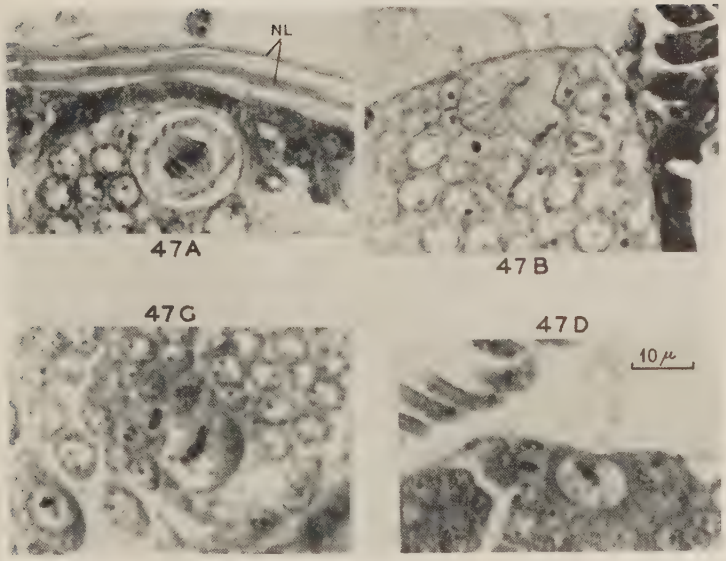
45b

46a

46b



44


NL
47A
47B
47C
47D
10 μ

THE DESCRIPTION OF THE FEMALE SEX OF PTERINOXYLUS SPINULOSUS, WITH NOTES ON STRIDULATION IN THE FEMALE SEX OF THIS GENUS (ORTHOPTERA; PHASMATIDAE; PHIBALOSOMATINAE)

BY JAMES A. G. REHN

Curator of Insects, Academy of Natural Sciences of Philadelphia

In the Autumn of 1956 Dr. P. F. Scholander, Professor of Physiology at the Institute of Zoophysiology of the University of Oslo, Norway, asked my assistance in the determination of a species of phasmid which a field party from the Institute had obtained January 12, 1956, while making investigations on Barro Colorado Island, in the Canal Zone of Panama. The actions of this insect while alive understandably interested those who secured it, and the specimen, preserved in alcohol, was later sent to me for study and presented to the Academy. It proved to be a fully adult female specimen of a species of the relatively rare genus *Pterinoxylus*, and the notes and observations here presented add materially to our knowledge of the genus.

The genus *Pterinoxylus* was described by Serville in 1839,[1] and based on his new species *difformipes*, founded on a female from "Amérique méridionale." Westwood in 1859[2] regarded Serville's species as identical with Burmeister's *Haplopus eucnemis* of 1838,[3] described from "Innern Brasiliens." Westwood also supplied a full-sized figure made from Burmeister's type in the Berlin Museum, as well as a redescription of the species. In 1889 Kirby[4] described an additional species of the genus from Dominica as *P. crassus*. This latter species apparently has not been taken in recent years, and nothing additional on it has been published since its description.

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[1] Hist. Nat. Ins., Orth., pp. 226, 227.

[2] Catal. Ins. Brit. Mus., Pt. 1, Phasmidae, p. 90, pl. XXXVI, fig. 10.

[3] Handb. der Entom., II, abth. II, pt. 1, p. 577.

[4] Ann. Mag. Nat. Hist. (6) III, p. 502.

In 1904 the present author reported[5] three immature individuals of the genus, representing both sexes, from Tucurrique and Turrialba, Costa Rica, as *eucnemis* with a query, stating at the time that Westwood's figure of Burmeister's type appeared to be of a species having the femoral and tibial lobes more rounded and not as distinctly triangularly acuminate as in the Costa Rican individuals. In 1908 in his classic work on the Phasmatidae with Brunner, Redtenbacher[6] placed under *Pterinoxylus* three species, *eucnemis* Burmeister (for which he used the subsequently published name *difformipes* of Serville), *crassus* Kirby (with no new information), and a new species *spinulosus* described from the adult male, plus a larval female, from "Chiriqui, Panama (Coll. m[ihi], Coll. Godman)." Under the first mentioned species he listed the following localities: "Sudamerika (Serv. Westw.) Brasilien (Burm.); Surinam (Coll. m[ihi]); Costa Rica (Mus. Paris); Guatemala (Coll. Godman)." In 1908 in the section of the "Biologia Centrali-Americana" on the Phasmatidae,[7] arranged by Shelford, the full localities for the Godman and Salvin material, examined and reported as *difformipes* (= *eucnemis*) by Redtenbacher, are given as: *Guatemala,* Chacoj in Vera Paz, and *Panama,* Chiriqui. Shelford also said that *difformipes* was "represented in the Godman and Slavin collection by four larvae only," and that the series of *spinulosus* consisted of "1 ♀ larva, ♀ type." The sex given for the latter by Shelford is clearly a lapsus calami, as Redtenbacher's description and figure were clearly based on the male sex, which is fully alate. It is thus evident that of the Central American material which was recorded as *difformipes* (= *eucnemis*) by Redtenbacher all certainly were immature, doubtless like those reported by me in 1904, except possibly the Paris Museum specimen recorded from Costa Rica, and of which the sex or condition was not stated. In 1923 Hebard reported a male specimen of the genus which he determined as *spinulosus* from "Panama."[8] This individual,

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[5] Proc. Acad. Nat. Sci. Phila., 1904, p. 61.

[6] Die Insektenfamilie Phasmiden, III, p. 428, pl. XX, fig. 3 (latter of *P. spinulosus* ♂).

[7] Biol. Cent.-Amer., Orth., II, p. 365.

[8] Trans. Amer. Entom. Soc., XLVIII, p. 361.

which had been dried from alcohol, belongs to the United States National Museum, and by the courtesy of the officials of that institution is now before me. It is an adult male and fully referable to Redtenbacher's *spinulosus*.

This resumé of the systematic background is essential to understand the discussion here presented. The specimen sent to me by Dr. Scholander and his colleagues clearly represents the previously undescribed adult female of Redtenbacher's *Pterinoxylus spinulosus,* of which I find the Academy series also has two previously undetermined female individuals both from Panama, although the only male which I have seen is the above-mentioned one reported by Hebard in 1923. The fully alate male, however, differs very greatly in appearance from the female, and was figured by Redtenbacher.

A comparison of these females with Westwood's figure of Burmeister's type of *eucnemis*, also a female, shows numerous differences, some of which conceivably may be due to generalizations in Westwood's figure, but of this we have no positive proof, and Serville's detailed description of the female described as *difformipes* very largely supports the Westwood figure. However, I am here giving the first illustration of the female of *spinulosus* (fig. 1), and also a reproduction of Westwood's figure of the type of Burmeister's *eucnemis* (fig. 2).

The following comments as to the differences in the female sex between the two species have been drawn from the *spinulosus* material before me, Westwood's figure of the above-mentioned type, his description of the same, and Serville's description of his *difformipes* (also based on the female sex). The pronotum is smoother in *spinulosus,* and shows no marked nodes on it as figured by Westwood for *eucnemis;* the dorsal nodes on the tegmina are less pronounced and smaller in *spinulosus;* the third abdominal tergite bears paired spines mesad on its caudal margin, as well as the more lateral paired foliaceous lobes, each of these latter bearing two spiniform points, the seventh abdominal tergite has no distinct spines along its caudal margin as described for *eucnemis* by Serville, Westwood and Redtenbacher, instead merely low nodes, none of the other terminal tergites of the abdomen bear spines on their caudal margin as described by Serville

for the genotypic species; the elongate subgenital plate has its distal margin broad and biconcave to obtuse-angulate rather than broadly rounded as in *eucnemis*; the cephalic femora have the lamellation of their ventro-external margin more even in outline, broadening distad to a single preapical, rather rounded but subtrigonal lobation; the median femora have the internal (caudal) of the paired disto-dorsal lobes higher and more rounded, ventro-external margin of same lobate mesad and distad, but not spinose as figured by Westwood for *eucnemis*; median tibiae with disto-dorsal lobation longer and lower, occupying two-fifths of tibial length, proximo-dorsal lobation very low and rounded but distinct; caudal femora with disto-dorsal lamellato-lobation acutely produced; its height and prominence definitely greater than in Westwood's figure of *eucnemis,* ventral margin of same femora lacking true spines as shown for *eucnemis*; caudal tibiae straight with their disto-dorsal lamellate lobation higher and longer than shown for *eucnemis* and undivided except for the crenulations of its margin. The limb feature differences are equally evident in the nymphal female from Turrialba, Costa Rica recorded by me in 1904, which is now before me in the Academy series.

The following more detailed description of the female sex of *spinulosus,* which has been drawn from one of these before me, should prove of service to other students who may be dealing with this most interesting genus.

Female: Barro Colorado Island, Canal Zone, Panama. July 29, 1933. (J. D. and H. Hood.) [Academy of Natural Sciences of Philadelphia.] [9]

Size large (length of body, including subgenital plate, 172 mm.); form twig-like; surface areally subspinulose and with many areas of whitish sublichenose coloration.

Head subequal in breadth to the mesonotum, with a low transverse swelling placed half-way between the antennal bases and the base of the occiput, its surface with numerous low tubercles, occipital base with two pairs of rounded swellings, one pair on the occipital border itself, the other

[9] It is exceedingly difficult to set the tegmina and wings of females of this species to show the tympanal area at the base of the wings, also the convex contour of the wings makes their conventional spreading impossible. The specimen here figured and described presents most of the characteristics of the species better than the other two adult females now before me.

more lateral and virtually postgenal in position, a number of additional spiculate tubercles are scattered over the occipital dorsum and lateral aspects of the head; eyes little prominent, subcircular in basal outline; antennae when extended caudad reach to the caudal fourth of mesonotum.

Pronotum with its greatest breadth subequal to five-eighths of its length, which latter is slightly longer than the head, U-shaped transverse sulcation crossing the median longitudinal subsulcation almost in its middle, surface with no marked nodes but with a number of low asperities. Mesonotum 4.3 times as long as the pronotum, but faintly narrowing in breadth in cephalic third, its greatest breadth, which is at the caudal extremity, equal to less than one-fifth of its length, premedian group of nodes, which are apparently much more prominent in *P. eucnemis,* evident but low, mere knots of irregular strumose rugae, but slightly more evident than the many knob-like tubercles or rugulae which are scattered over the mesonotal dorsum, some linearly disposed, usually paired but not invariably so, an irregularly disposed and variably emphasized median carinula is also indicated. Metanotum with its length contained approximately three and one-half times in that of the mesonotum.

Tegmina subovate, reaching caudad to approximately the proximal third of the proximal abdominal tergite, apex broadly rounded, surface texture much as that of the body as a whole, the areolation of the venation relatively irregular, the elevated lappets or nodes dorsad of the alar articulations well marked, subvertical on their side toward the costal tegminal margin; ventral border of distal margin supplied with minute spicular nodules. Wings, when closed, projecting caudad of the tegminal apices a distance equal to twice the tegminal length, their surface when expanded is arcuately domed, its structure such that the wings can not be spread flattened except by distorting their form, costal margin of wing nearly straight in proximal two-thirds, moderately arcuate in distal third, apex of anterior field and adjacent portion of radiate field subtruncate, remainder of margin of radiate field moderately arcuate, anterior field with exposed distal section mortuifoliaceous as the body and tegmina, normally covered proximal portion with a shallow cup-like subconcave depression, apparently similar to but proportionately smaller than that in *P. eucnemis,* its border on the costal side sharply defined by the radius (apud Ragge 1955), which is markedly arcuate costad of the depression, the floor of which latter bears the proximal continuation of the venational elements of the remainder of the anterior field and their cross veinlets, the entire surface of the proximal part of the costal section of the wings, the veins of the humeral trunk in most of their length and the entire surface of the depression and the adjacent, more distal, section of the anterior field densely supplied with minute spicular nodules, which clearly serve a stridulatory purpose; radiate field of wing with the radiate veins each narrowly bordered laterad by parallel, appreciably thickened or stiffening sections of the wing membrane, which may reinforce or strengthen the radiate veins, and which conceivably could play some part in stridulation, the radiate veins, the

adjacent thickened section of the membrane and the thinner membrane itself with innumerable microscopic spicular points, much smaller than those structures found in the vicinity of the tympanal depression.

Abdomen essentially virgate, as a whole weakly narrowing distad, tergites two to nine meso-longitudinally with a closely placed median pair of carinulae which vary somewhat in emphasis and also in the degree to which they are straight or moderately sinuate, briefly expanding somewhat at the immediately proximal section of tergites third to eighth, the area between them becoming increasingly deeper and more incised distad, lateral of the median pair surface carinulations are present in two or three paired irregular but distinct lateral series on tergites three to nine, tergite three bears next to the distal margin at the end of the median pair of carinulae a pair of spines, and as parts of the first carinulate series laterad of the median pair a group of two or three acuminate, subspiniform lobes, with a pair of single smaller but similar lobes in the same position on the fourth tergite, seventh tergite moderately expanded disto-laterad, its greatest breadth there but little less than the median length of the same tergite, eighth and ninth tergites appreciably narrower than the seventh, slightly compressed; ultimate tergite slightly broader than median length, subcucullate, distal margin obliquely subtruncate dorsad of the cerci, mesad concave, surface of tergite more thickened and rugose laterad and distad than over most of the remainder of the surface; cerci very short, their apices but faintly surpassing the distal margin of the ultimate tergite, subdepressed, in outline as seen from the dorsum moderately acute, the external outline subarcuate, the internal nearly straight; subgenital plate with its ventral length subequal to that of the proximal three abdominal tergites, narrowly scaphiform, its lateral margins subparallel as seen from the dorsum, its dorsal interior deeply canaliculate proximad becoming shallower distad, distal margin subtruncate, its lateral angles subrectangulate, the immediate distal margin shallowly obtusely angulate emarginate, but somewhat irregular in outline.

Cephalic femora about five-eighths as long as the mesonotum, cephalic flexure occupying almost all of the proximal half, distad of this the dorsal lamellation is high and well marked, its margin erosulately undulate, accompanied on the external side by a carinulation which becomes more elevated distad, ventro-external (caudal) lamellation regularly increasing in depth distad, with its distal extremity erosulately concave; cephalic tibiae slightly shorter than the cephalic femora, of their four major carinate margins the external is quite broadly and in most part evenly lamellate but with several undulations which break the continuity of its form, the dorsal carination is supplied with a number of low and rounded sublobations; median femora nearly four-fifths as long as the cephalic ones, their dorsal surface with two carinulations, the external (or caudal) of which has a marked but semicircular preapical lobation, and two much smaller ones distad in decreasing size, the internal (or cephalic) dorsal margin has a similar but much smaller distal lobe and a smaller more proximal one

virtually paired with those of the external margin, ventro-internal (ventro-cephalic) margin with a distinct preapical and a median subtrigonal lobation, which are matched on the ventro-external (ventro-caudal) margin; median tibiae bearing solely on its dorsal surface at distal end a rather elongate lobation, occupying nearly two-fifths of the tibial length and with its outline serrulately rounded; caudal femora subequal to the cephalic femora in length, the dorsal margin with a marked distal acute unguiculiform lobation, the margin of which beneath the terminal "claw" is irregularly serrate, ventral margins of the caudal femora with a few serrations, these weak and irregular except for one on each margin shortly before the femoral apex; caudal tibiae with a distal lobation in the same position as on the median tibiae, but higher and shorter in length, with its margin serrulate.

Coloration.—Base tone ranging from as dark as bister to as pale as buffy brown, in the paler individuals the whole overlaid to variable degrees with patches of bister over the lighter general tone and with frostings or areal cloudings of lichenose white or creamy white, the whole producing a marked "dead twig" effect, while the localization of the lichenose areas does not agree in any of the three adult females before me; at the base of the eighth tergite are placed paired ocelliform spots of dull black, which apparently surround a pore in the tergal integument—this latter pattern is found in all three adult females seen. The tegmina, like the body and limbs, are markedly mortuifoliaceous in their coloration, as well as in structure, but the normally covered portion of the wings is quite different. The radiate field of the latter has the immediate area of the individual radiate veins bister, with the membrane between paler, nearer sayal brown (of Ridgway); the anterior field of the wing distad (i.e. its normally exposed section) is colored and mottled like the tegmina, but the proximal portion, and the area of the tympanum is definitely and contrastingly red, in the dried material being between nopal red and carmine (of Ridgway).[10]

In addition to the described specimen, two adult females are also before me, these bearing the following data:

Barro Colorado Island, Canal Zone, Panama; I, 12, 1956; (Berthe Ruud); [A.N.S.P.].[11]

Bruja Point, Canal Zone, Panama; X. 21. 1929; (James Zetek); [A.N.S.P.].

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[10] Miss Berthe Ruud kindly sent me a crayon sample giving the color of this area as she and her companions recalled it in life in the specimen sent to me for identification. This sample agrees fully with the color seen in the preserved individual here described. This latter has never been immersed in any liquid preservative.

[11] This is the specimen on which the following life observations were based.

The measurements (in millimeters) of the three females of *spinulosus* are as follows:

	Barro Colorado, C. Z., Panama (described specimen)	Barro Colorado, C. Z., Panama 1956 [11]	Bruja Point, C. Z., Panama
Length of body (including subgenital plate) ..	172.0	151.0	137.0
Length of pronotum ...	9.0	9.5	8.0
Length of mesonotum ..	39.5	34.5	29.0
Length of tegmen	15.0	12.5	13.0
Length of anterior field of wing	20.0	18.5	20.5
Length of cephalic femur	25.0	24.0	22.5
Length of median femur	19.5	17.0	16.5
Length of caudal femur	25.5	23.5	22.0
Length of caudal tibia ..	19.0	16.5	... [12]
Ventral length of subgenital plate	28.5	26.5	25.5

In my first communication from Dr. Scholander apropos of the specimen later sent by him, he stated that "when excited it erected a pair of orange and black wings, and chirped audibly." The specimen was retained alive for some time and used for respiratory measurements, which probably will be published at a future date. Desiring to secure more specific information both on its stridulations and on the exact color of the hind wings, which had been largely destroyed by the alcoholic preservation of the specimen I requested some details on these matters. Miss Bertha Ruud, a graduate student at the Institute of Zoophysiology, who had collected the specimen, most kindly has sent me some observations on the actions of the specimen, which was kept alive for about ten days, as well as a note on the color of the hind wing in life. With her kind permission I am quoting from several letters which passed between us, and which add to the exceedingly limited information available on phasmid stridulation.

"The phasmid was taken on January 12, 1956 about noon, at the end of the rainy season. As I was sitting on the ground in the rain-forest of the island, I observed it clinging to my jeans.

[12] Tibiae of single remaining limb atrophied, perhaps regenerated.

I brought it to the laboratory and put it in a small cage. It was not until 3 or 4 days later, when we took it out of the cage for closer examination that we observed the small red wings. As the wings vibrated we heard a distinct stridulating (?) noise, not unlike a bumble bee or a distant airplane. The vibrations were intermittent and each period lasted for about 5 seconds with longer and irregular periods of rest. It was especially active in this respect when we irritated or stimulated it with a pencil. It died after about ten days, not later than January 22. As far as we could see, it took no food or water." In a subsequent letter, in reply to my request for advice on the unusual wing coloration, she wrote, "It is more than a year since we saw the phasmid alive, so I find it rather difficult to remember precisely what shade of red the wings, were, but I have consulted my friends here, and we agree upon a brick red, not unlike the sample" (which she had kindly appended and which I have matched with Ridgway's standards for use in the preceding description).

The sole information in past literature which I have been able to trace on the stridulation of phasmids, and based on this genus, was presented by Wood-Mason as a verbal comment at the November 7, 1877 meeting of the Entomological Society of London,[13] and which is as follows:

"Mr. Wood-Mason then announced the discovery of stridulating organs in Phasmidae, in species of *Pterinoxylus*, and in illustration of his remarks exhibited an impression of Westwood's plate of Serville's species *P. difformipes* [= *P. eucnemis* (Burm.)]. Here, as in the Crustacea [which he had been discussing] and some other arthropods, an apparatus working perfectly independently of its fellow was developed on each side of the body. The rough prominent basal portion of the costal nervure of the wings formed the rasp, in connection with which was developed a large oval 'speculum,' 'talc-like spot' or 'mirror.' The rasps were scraped by the sharp and hard front edges of the tegmina, the dome-like form of which seemed admirably adapted and probably did, to some extent, serve to increase the sound by resonance. In Serville's species, according to Westwood's figure,

[13] Trans. Entom. Soc. London, 1877, p. XXVIII (1877).

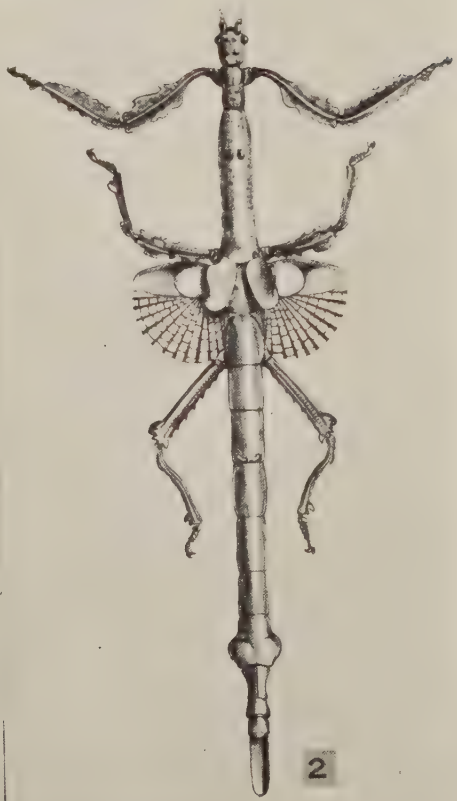
the stridulating apparatus appeared to be more highly developed, the mirror being more distinct and the tegminal cavities much more spacious. The males of the Pterinoxyli are unknown. We had here another case in which functional stridulating organs are present in females."

We are not advised in this note of the source of or locality for the material which Wood-Mason discussed, but presumably he considered it to be distinct from the species figured by Westwood (i.e. *eucnemis*). Whether he had an individual of *P. spinulosus* it is impossible to say, except that the latter species clearly has a smaller " speculum " on the wings than that figured by Westwood for *eucnemis*.

Explanation of Plate

Fig. 1.—*Pterinoxylus spinulosus* Redtenbacher, ♀, Barro Colorado Island, Canal Zone, Panama. About two-thirds of natural size.

Fig. 2.—*Pterinoxylus eucnemis* (Burmeister), ♀, reproduction of Westwood's 1859 figure of Burmeister's type. About three-fifths of measurements given in Westwood's description of the type.



REHN: PTERINOXYLUS

THE BIOLOGY OF *PANCHLORA NIVEA*, WITH OBSERVATIONS ON THE EGGS OF OTHER BLATTARIA

BY LOUIS M. ROTH AND EDWIN R. WILLIS

Pioneering Research Division, U. S. Army Quartermaster Research and Engineering Center, Natick, Massachusetts

BIOLOGY OF *Panchlora nivea*

Little is known of the biology of the pale-green Cuban cockroach, *Panchlora nivea* (Linnaeus). Various biological observations on purportedly different species of *Panchlora* may refer to *P. nivea*. Rehn and Hebard (1927) listed seven names that have been used for West Indian species of *Panchlora*. These workers stated: "There is a strong possibility that in most cases they relate to *P. cubensis*, the dominant West Indian species, but their arbitrary reference to that species would hardly be warranted." Gurney (1955) has shown that *P. cubensis* Saussure is a synonym of *P. nivea* (Linnaeus). Hebard (1917) stated that Shelford, after examining the types, placed *P. virescens* in synonymy under *P. nivea*. Rehn and Hebard (1927) stated that without more explicit information on the type, *P. viridis* (Fabricius) must be considered to be an unidentifiable species of the genus. However, Hebard (1917) identified as *P. cubensis* (= *P. nivea*) many of the adventives that had been reported by others as *P. viridis*. Where the synonymy is evident, we have discussed the species as *P. nivea;* where it is not, we have retained the name assigned by the original observer.

Panchlora nivea is the dominant species of the genus in the Greater Antilles, and it is widely distributed in Mexico, Central America, and northern South America; it is the one most frequently encountered adventive in the eastern United States, being regularly transported to this country in bananas (Rehn and Hebard, 1927). According to Hebard (1917) *P. nivea* is found established in the United States only in the vicinity of Brownsville, Texas; it is essentially an out-of-doors tropical form that can not adapt itself to artificial surroundings, and which, he stated, can never become established north of the tropical areas of this country.

In Puerto Rico, *P. nivea* is found in the rotting trunks of palm or coconut trees where it feeds on the rotting brown fibers in which it tunnels (Seín, 1923; Wolcott, 1950). The nymphs are brown and resemble those of *Pycnoscelus;* they require 100 days to mature; the female produces 30 nymphs per oötheca (Seín, 1923). Scudder (1890) reported that *P. nivea* is viviparous and this was confirmed by Riley (1890, 1891). Riley reported that a female of this species gave birth to about 30 young. He dissected another female and found a semicircular-shaped oötheca containing about 44 eggs. The oötheca consisted of a thin membranous sheath which covered the basal half of the egg mass. Riley believed that hatching occurred in the genital pouch within the abdomen of the female and that this pouch was so large that the young could move about and undergo " postnatal development ". Hansen (1894) found a museum specimen of a female *P. " viridis "* which had an egg capsule protruding from the end of her abdomen. Bayford (1934) claimed to have observed *P. " viridis "* (or *P. exoleta* Burm.) giving birth to about 30 young, and stated that no oötheca was extruded, nor could he find one after dissecting the female. Davis (1930) stated that a female *P. nivea* kept in captivity gave birth to about 20 young without producing an egg capsule. He reared two males to maturity; one took a little over 6 months to mature, the other nearly 8 months. Shelford (1906) observed a live specimen of *P. nivea* which had an oötheca partially protruding from the end of her abdomen; the oötheca was " complete " as compared to the " incomplete " membrane in the specimen observed by Riley. Shelford concluded that in his specimen the egg mass was so large that it could not be retained entirely within the brood sac. Chopard (1938), probably taking his information from Riley and Shelford, stated that the oöthecal membrane of *P. " viridis "* and *P. nivea* is incompletely formed and tends to disappear.

The oöthecal membrane of *P. nivea* when first laid down covers nearly all of the eggs. It is possible that Riley's observation, that the membrane envelops no more than half of the eggs, was based on an oötheca in which the embryos were well developed; in this case the increase in the size of the developing eggs may have decreased the area covered by the oötheca. Actually, the

oötheca is so thin and practically colorless (except for light amber colored edges) that it is difficult to see the extent of the membrane (Plate XXII, fig. 9) unless the eggs and oötheca are separated (Plate XXII, fig. 10). Although Bayford (1934) claimed that no oötheca was extruded by *P.* " *viridis* " at parturition, it is possible that he observed the young shortly after they were born by which time they may have eaten the oötheca and embryonic membranes, a common practice among " ovoviviparous " cockroaches.

We have established a colony of *Panchlora nivea* from a single female collected by Edna Roth, May 12, 1956, on bananas in a store in Framingham, Massachusetts. After 26 days in the laboratory, kept at 24 C. and 50 to 60 per cent R. H., this cockroach gave birth to 60 young. Nineteen days after giving birth, the female was observed with an oötheca protruding beyond her wing tips; within 55 minutes she had completely retracted the oötheca into her brood sac. Sixty days after oötheca formation this female gave birth again. She died October 12, 1956, after having lived 153 days in the laboratory; she fed on banana skins and Purina Dog Chow checkers. At autopsy we found a J-shaped oötheca, containing 53 eggs, in the brood sac. The oötheca was tightly enveloped by the uterus which filled most of the body cavity.

The ovipositional behavior of *Panchlora nivea* is similar to that found in species of *Gromphadorhina, Pycnoscelus, Nauphoeta, Leucophaea*, and *Blaberus* (Roth and Willis, 1954). The female *Panchlora* that Shelford (1906) reported as carrying an exposed oötheca was either in the act of ovipositing or had prematurely extruded the egg case. Premature extrusion of the oötheca by cockroaches that incubate their eggs in a brood sac may occur when they are killed (Roth and Willis, 1954); this probably explains Hansen's (1894) observation (see above).

Contrary to Riley's opinion the nymphs, during normal birth, do not move about in the genital pouch after the eggs hatch. We have observed birth once in *P. nivea*, and the act of parturition in this species is no different from that in species of *Leucophaea, Nauphoeta*, etc.; the oötheca containing fully developed eggs is re-extruded, and once the embryos are clear of the confines of the

female's body they free themselves completely from their enveloping membranes and drop from the oötheca. Apparently under abnormal conditions it is possible for an embryo to hatch within the brood sac. When one of our females died, she partly extruded her oötheca. None of the exposed embryos were able to free themselves from the enveloping membranes and oötheca. On dissecting this female we found that the oötheca had broken into two parts; the anterior part, containing ten embryos, remained tightly invested by the anterior end of the brood sac. One embryo had shed its embryonic skin almost completely; only its tarsi were still encased. This nymph had already become tanned, and it is conceivable that at a later stage of development it might have shed its skin completely and moved about in its cramped quarters. This abortive hatching was possible because the broken oötheca, having separated, left an empty space in the brood sac which was prevented from collapsing by the eggs that distended the anterior and posterior parts of the uterus. An empty brood sac contracts to a fraction of its distended size.

Twenty-three nymphs from the first litter of 60 were reared to maturity. Males (N = 10) [1] matured in an average of 144 ± 8.0 [1] days and females (N = 13) in 181 ± 6.3 days. The mean number of nymphs per litter from 14 births was 46.1 ± 2.4 (range = 28 to 60). The mean time to the birth of the first litter for seven females isolated after mating was 55.3 ± 1.8 days (range = 50 to 62 days). If we allow about a week after mating for oviposition to occur, then embryogenesis takes an average of about 48 days at 24° C.; it will be recalled, however, that the first female used to establish the *P. nivea* colony, gave birth 60 days after oöthecal formation. Three of the seven females gave birth again 63.3 ± 2.9 days after the first birth. One female gave birth to a third litter.

We have observed the mating behavior of *P. nivea* several times. When confronted with six-day-old virgin females, males that are several days old simply run rapidly around behind the female, back up to her (Plate XXII, figs. 1, 2), and quickly make connection. The final mating position, during which time the

[1] N = number of individuals from which mean values were computed. The figures at the right of ± are standard errors.

spermatophore is transferred, is end to end with the heads of both individuals facing in opposite directions (Plate XXII, fig. 3). The average time spent in copulo was 40 ± 2.4 minutes (range = 30 to 46 minutes, N = 7). Six-day-old females mated readily; the males mated with these without any apparent preliminary courtship. The female does not feed on a secretion on the male's tergum nor does she assume the superior position prior to copula, as has been reported for several other species (Roth and Willis, 1954). Females four and five days old did not mate as readily as those six days old. With these younger females, the male behaved differently. He moved around the female slowly and stopped near the end of her abdomen where he rocked from side to side and at the same time arched his abdomen downwards so that his wings were held slightly away from his body. He then slowly backed up toward the end of the female's abdomen and remained quiescent in this position for some time. The younger female may actively resist the male's attentions by kicking with her hind legs or by running away.

The precopulatory position in *Panchlora*, in which the male simply backs up to the female and makes connection, differs from that known for all other cockroaches in which mating has been observed. Although Ramme (1923) stated that the male of *Ectobius* backed up to the female, this was questioned by us (1957) and found not to be true in *Ectobius pallidus*. Rau (1922) made a single field observation on the mating of *Parcoblatta pensylvanica* (DeGeer) and claimed that the female was the aggressor and attempted to back under the male (this would be a male superior pose). This precopulatory position is highly doubtful. We have observed the courtship of *Parcoblatta virginica* (Brunner); this species behaves like other species of cockroaches in which the males have a tergal gland. The male of *P. virginica*, after touching the female with his antennae, raises his wings to about a 45° angle; he may remain in this position for a time if the female that he is courting does not respond. If the female begins to feed on his tergal secretion, he raises his wings to 90°, and when her mouthparts reach his first abdominal segment, he pushes backwards and grasps her genitalia. The pair then assume a position, typical of blattids, with their heads facing in

opposite directions. Males of *P. virginica* are attracted to courting males and feed on the male tergal secretion just as the females; this feeding stimulates the courting male to attempt copulation.

In practically all species of cockroaches, the female is above the male just prior to genital connection. The only exceptions so far as we know, are *Panchlora nivea* and *Pycnoscelus surinamensis* (Linnaeus).[2] In this latter species we did not observe any courtship by the male; he simply climbed onto the back of the female and twisted his abdomen down and under that of the female (Plate XXII, figs. 4-6); connection was readily made from this male superior pose, somewhat like the behavior of grasshoppers. After connection has been made, the final mating position (Plate XXII, figs. 7, 8) is similar to that of other cockroaches. The mean time spent in copulo by *Pycnoscelus* was 23 ± 1.2 minutes (range = 15 to 26 minutes, N = 8), during which time the spermatophore was transferred to the female.

Water Relations of the Eggs of Some Blattaria

Recently (1955) we discussed the water uptake by cockroach eggs and showed that the initial water content of eggs and oöthecae of species that incubate their eggs in a brood sac is considerably lower than the water content of the oöthecae and contained eggs of oviparous species. Table 1 gives the percentage of water not previously reported in the newly formed oöthecae and eggs of seven species of cockroaches. The relationship of a relatively low initial water content in the eggs and oöthecae of false ovoviviparous cockroaches in comparison with the oviparous forms (except *Ectobius pallidus*) is again borne out. Table 2 shows the changes with age in water and dry matter content of eggs of *Panchlora nivea* and two species of blaberine cockroaches which also incubate their eggs in a brood sac. The water content of the eggs of these species increased with age but there was no corresponding increase in dry matter which is so characteristic of embryonic development in *Diploptera punctata* (Roth and Willis, 1955a).

[2] *Pycnoscelus surinamensis* is parthenogenetic in the United States and apparently no males occur in nature in this country. We obtained three males which were reared from nymphs that were accidentally included in a shipment of *Diploptera punctata* (Eschscholtz) from Hawaii. A bisexual colony of *Pycnoscelus* has been established in our laboratory.

TABLE 1. Water content of newly formed oöthecae and their enclosed eggs from several species of cockroaches

Species and type of oviposition behavior	Water content (%) ± S. E.[1] of oöthecae and eggs	N[2]
Oviparous species which deposit and abandon the oötheca shortly after its formation:		
(1) *Ectobius pallidus* (Olivier)	40.0 ± 0.61	5
(2) *Neostylopyga rhombifolia* (Stoll)	64.3 ± 0.61	5
(3) *Parcoblatta virginica* (Brunner)	56.9 ± 0.68	5
(4) *Periplaneta brunnea* Burmeister	64.5 ± 0.43	5
False ovoviviparous species which extrude then retract the oötheca and carry it internally until the eggs complete development:		
(1) *Blaberus craniifer* Burmeister	36.0	1
(2) *Byrsotria fumigata* (Guérin)	34.7 ± 0.56	3
(3) *Panchlora nivea* (Linnaeus)	37.0	1

[1] S. E. = standard error
[2] N = number of oöthecae

Ectobius pallidus overwinters in the egg which seems to undergo diapause. Sometime before hatching, the eggs pick up water which causes the oötheca to swell (Roth and Willis, 1957). Nothing is known about the rate of uptake of water by the eggs of this species. On April 16, 1957, some overwintering oöthecae and a few nymphs (older than first instar) of *E. pallidus* were collected in Plymouth, Massachusetts. These oöthecae had not yet begun to swell visibly. The water content of five of these oöthecae was 41.0 ± 1.1 per cent. We had previously determined that the water content of newly formed oöthecae of this species (deposited in the laboratory) was about 40 per cent (Table 1). Thus the eggs of *Ectobius pallidus* apparently do not pick up water during the winter months since the water content of the eggs collected in the field in April (and which had been deposited in the previous summer or fall) was essentially the same as that of newly formed oöthecae.

The oöthecae were divided into two groups; one group was kept continuously on filter paper moistened with distilled water; the second group was removed from moist paper after nine days. The uptake of water is shown in text-figure 1A. Both groups of oöthecae rapidly increased in weight for four days; those eggs kept moist continuously (text-fig. 1A, solid line) then slowly increased in weight from the fourth to the twenty-first day at which

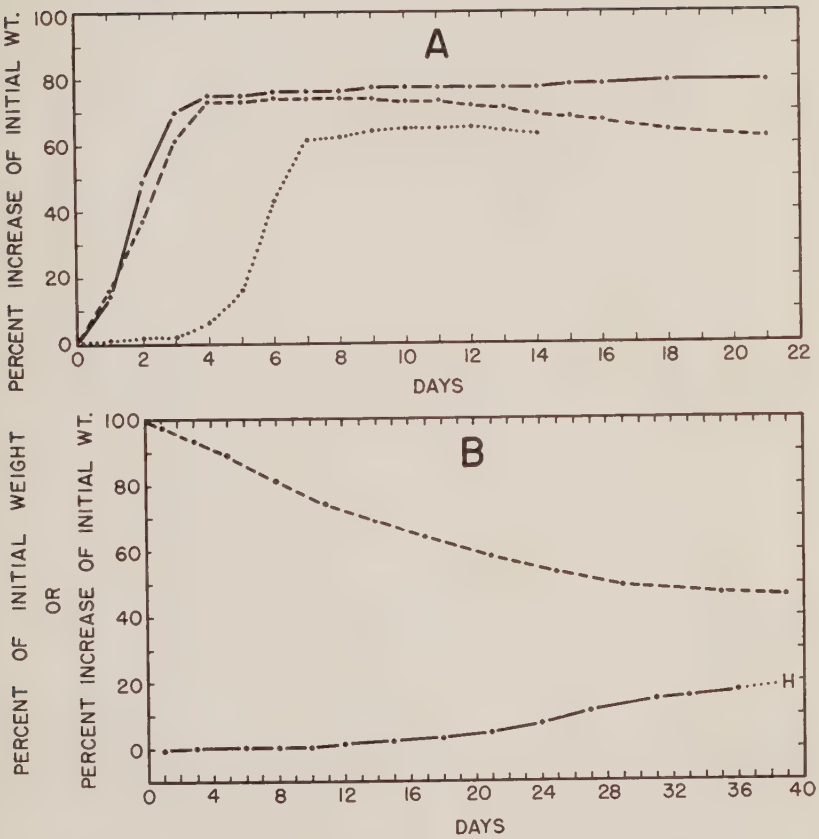
TABLE 2. Changes in wet weight, water, and dry matter of eggs of three species of false ovoviviparous cockroaches

Note: The actual ages of the eggs, except for the newly or recently formed oöthecae, were unknown. The eggs are arranged in order of increasing wet weight which, being correlated with development, represents an increase in age. The weight of the oötheca is included in the computations. All values were determined from one oötheca for each wet weight listed.

Species	Milligrams Per Egg		
	Wet weight	Dry Matter	Water
Blaberus craniifer	13.2 [1]	8.4	4.8
	19.8	7.6	12.2
	25.4	7.1	18.3
	25.6	7.4	18.2
	30.0 [2]	8.2	21.8
Byrsotria fumigata	13.1 [1]	8.6	4.5
	15.3 [1]	9.8	5.5
	16.0 [1]	10.6	5.4
	27.4	8.8	18.6
	27.9	9.8	18.1
	28.4	7.8	20.6
	29.4	9.4	20.0
Panchlora nivea	0.4 [1]	0.3	0.1
	0.7	0.2	0.5
	0.8	0.2	0.6
	1.0 [2]	0.3	0.7

[1] Newly or recently formed oöthecae.
[2] Well-developed embryos.

time the eggs began to hatch. It is estimated from known dry weights of oöthecae that at the time of hatching the oöthecae and eggs of group one contained about 75 per cent water. The second group of oöthecae (text-fig. 1A, broken line) similarly increased in weight until the ninth day. After the ninth day the eggs were placed on dry filter paper and they began to lose water gradually. However, in spite of this water loss the eggs in these oöthecae hatched on the twenty-second and twenty-third days. It is apparent that if sufficient moisture is absorbed, the eggs may subsequently lose some water, when subjected to dry conditions, but still complete development and hatch.



Text-figure 1.—A. Uptake of water by eggs of *Ectobius pallidus*. The oöthecae had overwintered in the field and were taken into the laboratory on 16 April, 1957. The axis of abscissas represents the days after the oöthecae were first placed on filter paper moistened with distilled water. The plotted points are mean values.

.——.= Six oöthecae kept on moistened paper until the eggs began to hatch on the twenty-first day.

.– – –.= Five oöthecae kept on moistened paper for nine days and then kept on dry filter paper.

. . . . .= One oötheca kept on moistened filter paper for fourteen days; see text.

B. Oöthecae of *Parcoblatta virginica* deposited in the laboratory. The axis of abscissas represents the age of the oöthecae. The plotted points are mean values.

.——.= Five oöthecae kept on moistened filter paper; the change in weight is expressed as the per cent increase of the initial weight. The last weighing was made on the thirty-sixth day and the eggs hatched (H) on the thirty-ninth day.

.---.= Ten oöthecae kept on dry filter paper at 50 to 60 per cent relative humidity. The loss in weight is expressed as a percentage of the initial weight. None of the eggs hatched.

A single oötheca behaved somewhat differently from the others; its weight changes are plotted separately (text-fig. 1A, dotted line). This oötheca showed very little increase in weight for the first three days on moist filter paper, but after the third day it began to pick up water more rapidly. Apparently at the time this oötheca was collected, the eggs had not reached the stage in development when they begin to absorb water through the oötheca. By the fourth day water began to be absorbed, and the subsequent weight curve is similar to the others described previously. After the twelfth day on moist paper, this oötheca began to lose weight, so it was dissected on the fourteenth day; many of the eggs were well developed having dark eye spots, but some embryos apparently had died and therefore had begun to lose weight.

In the field, the eggs of *Parcoblatta virginica* are deposited in relatively moist situations, under logs, bark, etc. In the laboratory, the female usually deposits her oöthecae on the moist cotton stoppers of vials containing drinking water. Those eggs not deposited on the moist cotton do not develop at room humidities and the oöthecae frequently collapse. This is similar to the behavior of the eggs of *Cariblatta lutea minima* Hebard.

The initial water content of oöthecae and eggs of *P. virginica* is about 57 per cent (Table 1). After two weeks, when kept on moist filter paper, the eggs begin to absorb water through the oötheca and continue to do so at a slow uniform rate, as represented by weight gain (text-fig. 1B, solid line), until hatching occurs on the thirty-ninth day. It is estimated that at the time of hatching the oöthecae and eggs contained about 67 per cent water. If the eggs are kept on dry filter paper at 50 to 60 per

cent R. H., water is lost steadily, as represented by weight loss (text-fig. 1B, broken line), and the eggs fail to develop.

The oöthecae of *P. virginica* differ from those of some other oviparous species (e.g., *Blatta orientalis, Periplaneta americana*) in apparently not possessing an impermeable coating which retards loss of water from oöthecae that are exposed to relatively dry conditions. The eggs of *P. virginica* do not undergo diapause; in this respect they apparently differ from the eggs of *Ectobius pallidus*.

Summary

Panchlora nivea extrudes its oötheca during formation and then retracts it into a brood sac where the eggs develop. When the embryos mature, the oötheca is re-extruded; the nymphs free themselves from their enveloping membranes, as the oötheca is forced from the brood sac, and drop from the female. One mating enabled a female to produce three litters. The mean number of nymphs per litter was 46. Embryogenesis took about 48 days at 24° C. Male nymphs matured in an average of 144 days and females in 181 days. The mating behavior of *P. nivea* differs from that which has been observed in other cockroaches in that the male backs up to the female to make genital connection, and the female does not feed on any secretion on the male's tergum. Another peculiar mating behavior among the Blattaria is that of *Pycnoscelus surinamensis*, the male of which makes connection with the female after climbing on her back. The final mating position of both *Panchlora* and *Pycnoscelus* is similar to that of other cockroaches; the sexes, with genitalia joined, face in opposite directions.

The water contents of oöthecae and eggs, not previously reported for several species of cockroaches are given. The eggs of *Panchlora nivea, Blaberus craniifer,* and *Byrsotria fumigata* increase in water content, but not dry matter, during embryogenesis. The eggs of *Ectobius pallidus* overwinter in the field with essentially no change in water content. Oöthecae of *E. pallidus* that had overwintered in nature were brought into the laboratory and kept moistened; they absorbed water rapidly for four days and then increased in weight slowly until the twenty-first

day when the eggs hatched. The oöthecae of *Parcoblatta virginica* are deposited in moist situations. In the laboratory, eggs of *P. virginica* that were kept moist began to absorb water after two weeks and increased in weight slowly until hatching on the thirty-ninth day. When the oöthecae of *P. virginica* were kept at 50 to 60 per cent relative humidity, the eggs lost water steadily and did not hatch.

Acknowledgments

We thank Dr. Barbara Stay for preparing the specimens and taking the photographs for figures 9 and 10, and for collecting, together with Roger Swain, the oöthecae of *Ectobius pallidus;* and Dr. Ashley B. Gurney, United States National Museum, for identifying our specimens of *Panchlora nivea.*

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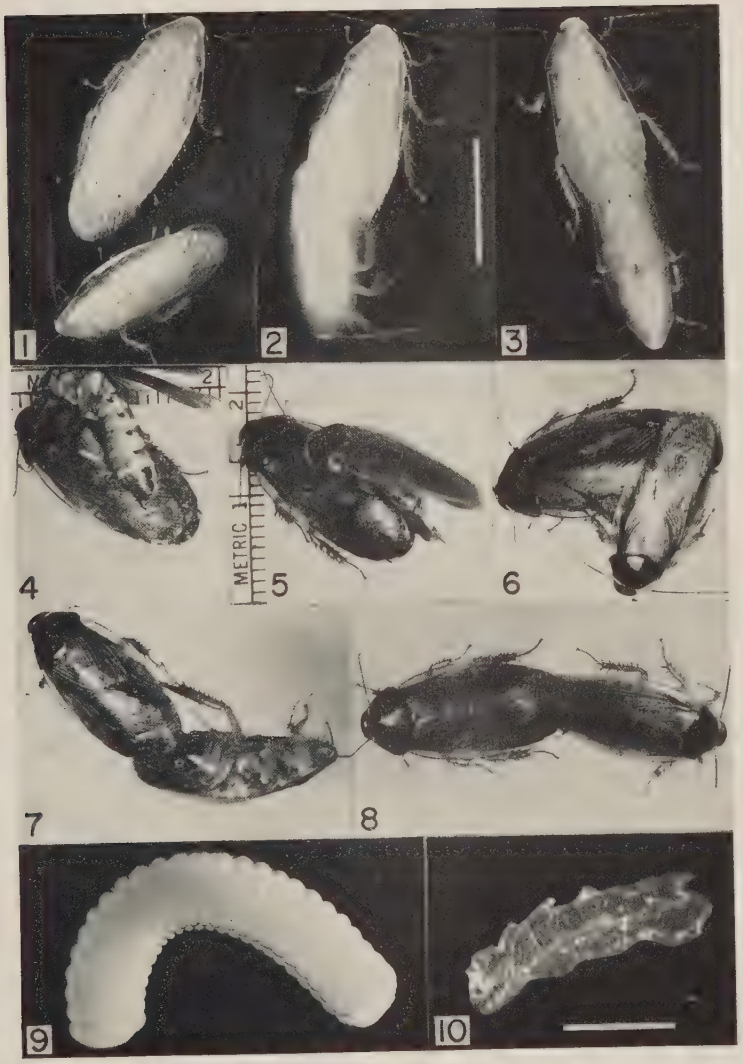
EXPLANATION OF FIGURES

PLATE XXII

Figs. 1-3.—*Panchlora nivea.* 1. Male moving around to posterior end of female. 2. Male (blurred) backing into female and making connection. 3. Pair in copulo. Vertical bar = 1 cm.

Figs. 4-8.—*Pycnoscelus surinamensis.* 4-6. Male on female attempting to make connection. 7. Pair connected, with male twisting around to assume an upright position. 8. Final mating position.

Figs. 9-10.—*Panchlora nivea.* 9. Oötheca and eggs removed from female. 10. Thin oöthecal membrane separated from the enclosed eggs. Horizontal bar = 3 mm.



ROTH AND WILLIS: PANCHLORA NIVEA

THE NEOTROPICAL KATYDID GENUS ROSSOPHYLLUM (ORTHOPTERA; TETTIGONIIDAE; PHANEROPTERINAE)

BY HAROLD J. GRANT, JR.

Assistant Curator of Entomology
Academy of Natural Sciences of Philadelphia

While determining recent collections of South American Orthoptera, several new genera and species of phaneropterine katydids have come to my attention. The first of these to be described is the genus *Rossophyllum*.

Thanks are due Edward S. Ross, California Academy of Sciences and Carl W. Rettenmeyer, University of Kansas for permitting me to study Orthoptera collected by them. The work was also advanced through the cooperation of T. H. Hubbell and T. J. Cohn, Museum of Zoology, University of Michigan, A. B. Gurney, United States National Museum, G. E. Wallace, Carnegie Museum and J. C. Pallister, American Museum of Natural History, all of whom loaned specimens from collections in their care. Finally, I wish to thank Dr. Max Beier, Natural History Museum of Vienna, for comparing one of the species studied with Brunner's type of *Microcentrum colosseum*.

Specimens recorded below have their ownership indicated by the following symbols: A.M.N.H. –American Museum of Natural History; A.N.S.P.—Academy of Natural Sciences of Philadelphia; C.A.—California Academy of Sciences; C.M.—Carnegie Museum; U.M.Z.—University of Michigan Museum of Zoology; U.S.N.M.—United States National Museum; V.—Natural History Museum of Vienna.

In the following descriptive work I have utilized the nomenclature of wing veins suggested by Ragge (1955). Certain measurements used below require some explanation as follows: eye depth —the greatest dorsoventral dimension of the eye in lateral aspect and measured at right angles to the long axis of the body; eye width—the greatest dimension of the eye in dorsal aspect and measured at right angles to the mesal border of the eye where it joins the head; interocular width—the distance between the eyes

from the point where they join the vertex anteriorly and at right angles to the long axis of the body; interantennal width—the distance between the mesal borders of the rims around the antennal sockets (scrobes); total body length—the distance between the frons and the tip of the posterior wings (when folded).

ROSSOPHYLLUM new genus

Diagnosis.—Head dorsally round, highly domed, broad. Wings with alternating green and diaphanous bands. Posterior femora about 7 times longer than broad, with 12-17 outer ventral spines and 6-9 inner ventral spines.

Description; head.—Dorsally rounded in lateral aspect; vertex domed, its dorsal surface about .75 times the depth of an eye higher than the dorsal surface of the eyes. Interocular width of vertex 3 times or more the width of one eye. Vertical and frontal fastigia confluent, their jointure marked by a very shallow, transverse straight sulcus. Vertex punctate, without a median sulcus. Eyes small and weakly protrusive.

Pronotum.—Anterior margin sinuate, with a low, blunt, medial projection. Posterior margin broadly rounded. Pronotal lobes about 1.3 times broader than deep. With paired, rather deeply impressed, dorso-lateral, transverse sulci anterior of the mid-point. Lateral margins, from above, divergent caudad. Lateral carinae rounded. Punctate throughout.

Wings.—Anterior wings 1.8 to 3 times longer than broad. Color green, with a series of 5 or 6 diaphanous bands obliquely aligned (dorso-posterior to ventro-anterior). Venation normal, archedictyon less dense in diaphanous bands. Posterior wings hyaline (except in exposed, posterior portion); uncolored.

Legs.—Inner ventral face of anterior femora with 4 to 7 spines. Posterior femora slender, 6.7 to 7.3 times longer than broad; with 12 to 17 spines along entire outer ventral border and 6 to 9 spines on distal half of inner ventral border.

Abdomen.—Terminalia simple. Cerciform processes lacking. Male cerci little specialized. Male supra-anal plate triangularly produced. Ovipositor short, distally crenulate or smooth on all margins.

Type species, *Rossophyllum clausum* n. sp.

Discussion.—*Rossophyllum* is closely related to both *Lobophyllus* Saussure and *Ischyra* Brunner while showing slightly less affinity to *Microcentrum* Scudder. It may be separated from all of these by the distinctive pattern of coloration found on the anterior wings. It differs from *Lobophyllus* in having the head more highly domed, the posterior femora slightly more elongate (7 times longer than broad, as opposed to 5.3-6.5 times longer

than broad) and in possessing an average smaller number of spines on the ventral borders of the posterior femora (inner ventral face 6-9, as opposed to 9-10; outer ventral face 12-17 as opposed to 22-23). It may be distinguished from the poorly known genus *Ischyra* in virtually lacking a median sulcus on the vertex (in a few of the specimens studied, the sulcus was present in a most obsolete condition) and possessing a broader and more extensive costal area in the anterior wings. From *Microcentrum* it differs in having the vertex more highly domed and the vertical and facial fastigia hardly interrupted by a transverse sulcus at their point of contact. In addition, the interantennal width of the head is conspicuously less broad in nearly all species of *Microcentrum*. Species of *Rossophyllum* could be confused only with *M. erosum* Brunner and *M. elephas* Brunner. From the first of these, all species of the present taxon differ in having the ventro-external border of the median femora armed for their entire lengths instead of possessing just two or three distal spines. From *elephas* (which is known to me through the description alone) one can rely on the color and pattern of the fore wing only as a means of separation since this species is said to possess opaque anterior wings.

The most distinctive feature of the genus, the broad diaphanous bands of the anterior wings, is found, as far as I am able to determine, in only one other phaneropterine genus—*Arnobia* Stål, known from Borneo only. The morphology of this character is interesting. In the green bands the archedictyon is quite dense with small crowded cells and raised green veins. In the diaphanous fasciae, the archedictyon is loose with larger cells and weakly raised whitish veins. The different areas are sharply delimited, but the progression from one to the other is slightly gradual in the anterior portion of the green bands.

Distribution.—The known range of *Rossophyllum* extends from the Canal Zone, Panama, south to Cochabamba, Bolivia in the west. In the east it is found in the states of Parana and Santa Catharina, Brazil.

It is a pleasure to name this genus after Edward S. Ross, Curator of Insects at the California Academy of Sciences, whose collection of Peruvian Orthoptera first drew my attention to its existence.

Key to the Species of Rossophyllum

1. Veins MA_2 and MA_3 of anterior wing connected by a prominent cross vein (fig. 12) ..... *Rossophyllum clausum* n. sp.
   Veins MA_2 and MA_3 of anterior wing not connected by a cross vein (figs. 11 and 13) 2
2. Vertex and frons coarsely punctate; total body length/length of posterior femur ratio more than 3:1; larger, total body length 65 mm or more. (Known from males only.) ..... *Rossophyllum sentum* n. sp.
   Vertex and frons nearly smooth, with only occasional, weak punctures; total body length/length of posterior femur ratio less than 3:1; smaller, total body length 60 mm or less. .. *Rossophyllum colosseum* (Brunner)

Rossophyllum clausum n. sp. Plate XXIII, A

Diagnosis.—This species is intermediate in size between the smaller *R. colosseum* (Br.) and the larger *R. sentum* n. sp. It may be separated from either of these by an examination of the anterior media vein (MA) of the fore wing which has branches MA_2 and MA_3 connected by a strong cross vein (fig. 12). It is also unique in lacking areas of darker pigmentation in the diaphanous fasciae of the anterior wing. Vein Rs of the fore wing appears to be absent in both sexes (fig. 12). The relationship of *R. clausum* to its congeners may be quite distant because of the venational inconsistencies of its anterior wings.

Type—♂, Tingo Maria, Huanuco, Peru, X-1946 (Weyrauch), 670 m. [Acad. Nat. Sci. Phila. Type no. 5968.]

Description; head.—Vertex and upper portion of frons moderately punctate. Dorsum of vertex about three-quarters the depth of an eye higher than the dorsal surface of the eyes when viewed laterally. Interocular width of vertex about three times the width of one eye and about 1.7 times the interantennal width.

Pronotum.—Coarsely punctate throughout. Lateral margins rounded. Median, dorsal length about 1.3 times the greatest dorsal width (fig. 3).

♂, paratype (Caviuna), *R. sentum;* Fig. 5, dorsal outline, supra-anal plate, *R. colosseum* (Brunner); Fig. 6, dorsal outline, right cercus, *R. colosseum;* Fig. 7, dorsal outline, right cercus, ♂, paratype (Tingo Maria), *R. clausum;* Fig. 8, dorsal outline, right cercus, ♂, paratype (Caviuna), *R. sentum;* Fig. 9, left lateral outline, ovipositor, allotype, *R. clausum;* Fig. 10, ventral outline, subgenital plate, type, *R. clausum.* Scale line to the right of each figure is proportionate to 0.5 mm at this magnification except for figures 2 and 3 where it is equivalent to 1.0 mm.

Figs. 1-10.—Morphological aspects of species of *Rossophyllum*. Fig. 1, dorsal outline, supra-anal plate, ♂, paratype (Tingo Maria), *R. clausum;* Fig. 2, left lateral outline, pronotal lobe, type, *R. clasum;* Fig. 3, dorsal pronotal outline, type, *R. clausum;* Fig. 4, dorsal outline, supra-anal plate,

(cont. bottom of facing page)

Lateral lobes about 1.1 times deeper (dorso-ventrally) than broad in greatest dimensions (fig. 2).

Wings.—Ventation and shape of anterior wing as in fig. 12. Anterior wing approximately 2.4 times longer than broad. Posterior wings, when folded, exceeding anterior wings by about one-fifth the length of the former. Anterior wings angulate-rounded distally (fig. 12). Posterior wings acutely angulate distally.

Legs.—Anterior femora with 5-6 weak spines along inner, ventral margin. Posterior femora relatively short and slender, about 7.3 times longer than broad; with 12 poorly developed spines along entire outer, ventral border; inner ventral border with 7 poorly developed spines in distal half only.

Abdomen.—Subgenital plate as in fig. 10. Cerci with a small, distal tooth (fig. 2). Tenth abdominal tergite apically truncate. Supra-anal plate produced; medially sulcate (fig. 1).

Measurements.—Total body length, 53 mm; median length of pronotum, 6.7 mm; length of anterior wing, 39 mm; greatest breadth of anterior wing, 16 mm; length of exposed portion of posterior wing, 8 mm; length of posterior femur, 17.6 mm; greatest breadth of posterior femur, 2.4 mm.

Allotype.—♀, Chanchamayo, Junin, Peru, 11-VI-1948 (Schunke). [U.S.N.M.]

The following description is comparative to that of the male and notes only features of difference.

Size.—Larger.

Head.—Dorsum of vertex the depth of an eye higher than the dorsal surface of the eyes.

Wings.—Anterior wings of greater breadth, about 1.8 times longer than broad.

Legs.—Ventral spines of both anterior and posterior femora better developed. Number of spines on outer ventral border of posterior femur 13-15; of inner ventral border, 8.

Abdomen.—Ovipositor with smooth margins (fig. 9).

Measurements.—Total body length, 65 mm; median length of pronotum, 7.3 mm; length of anterior wing, 48 mm; greatest breadth of anterior wing, 26 mm; length of exposed portion of posterior wings, 9 mm; length of posterior femur, 20.8 mm; greatest breadth of posterior femur, 3 mm; length of ovipositor (base of subgenital plate to apex), 3.8 mm.

Paratypes (8♂, 1♀).

Peru: Tingo Maria, Huanuco, IX-1946 and X-1946 (Weyrauch), 670 meters, 3♂ [2 A.N.S.P., 1 A.M.N.H.]; same locality, 27-X, 16-XI and 20-XI-1954 (Ross and Schlinger), 3♂ [C.A.]; Iquitos, Loreto, 1♀ [V.].

Bolivia: Chaparé, Rio Cristal Mayu, Cochabamba, XII-1950 (Peña), 1800 meters, 1♂ [U.M.Z.]

BRAZIL: Hyutanahan, Rio Purus, Amazonas, III-1922 (Klages), 1 ♂ [C.M.].

Variation.—The type series exhibits very little variation in the characters utilized in the description. In size (males only) the total body length varies from 52-54 mm, length of anterior wing 39-41 mm, breadth of anterior wing 15-16 mm and length of exposed portion of posterior wings 7-8 mm. The number of spines found along the inner ventral margin of the anterior femur varies from 4-7, the count sometimes differing on either femur of a single specimen. Similarly, the number of spines on the outer ventral face of the posterior femur varies from 12-15 while those found along the inner ventral face vary from 7-9.

Rossophyllum sentum n. sp. Plate XXIII, C.

Diagnosis.—*R. sentum* is closely related to the following species but differs from it in a number of distinctive features. In size it is much larger than *R. colosseum*. Males (the only sex known) possess slightly broader anterior wings (2.6 to 2.8 times longer than broad as opposed to 3 times longer than broad in *R. colosseum*). The vertex and frons are coarsely punctate while these parts are nearly smooth in *colosseum*. Another differentiating character is the extent and pattern of pigmentation in the diaphanous bands which cross the fore wing. In *colosseum* these darker, minute spots are restricted to racemose clusters in the network of the archedictyon while the present species possesses more elongate patches of irregularly placed spots (see figs. 14 and 15).

The venational characters discussed under the diagnosis of *R. clausum* separate it from this species.

Type.—♂, Corupa (Hansa Humbolt), Santa Catharina, Brazil, XI-1944 (Maller). [A.M.N.H.]

Description; head.—Similar in form and sculpturation to the preceding species. Dorsum of vertex about .9 the depth of an eye higher than the dorsal surface of the eyes in lateral aspect. Interocular width of vertex about 4.2 times the width of an eye and about 1.5 times the interantennal width.

Pronotum.—Similar in form and sculpturation to the preceding species. Median, dorsal length about 1.2 times the greatest dorsal width. Lateral lobes about 1.2 times deeper (dorso-ventrally) than broad (greatest dimensions).

Wings.—Venation and shape of anterior wing as in fig. 11. Anterior wing about 2.7 times longer than broad. Posterior wings (when folded) exceeding anterior wings by about one-ninth the length of the latter. Posterior angulation of fore and hind wings as in fig. 11 and Plate XXIII, C. Pigmented areas of diaphanous bands in anterior wing as in fig. 14.

Legs.—Anterior femora with 5-6 moderately well-developed spines along the inner ventral face. Posterior femora about 7.2 times longer than broad; with 15-17 moderately well-developed spines along the entire outer ventral border; inner ventral border with 8-9 moderately developed, but weaker spines in distal half only.

Abdomen.—Subgenital plate similar to *R. clausum* (fig. 10). Cerci with a distal, lunate, sclerotic plate (fig. 8). Tenth abdominal tergite as in preceding species. Supra-anal plate as in fig. 4.

Measurements.—Total body length, 65 mm; median length of pronotum, 8 mm; length of anterior wing, 52 mm; greatest breadth of anterior wing, 19 mm; length of exposed portion of posterior wing, 6 mm; length of posterior femur, 19.2 mm; greatest breadth of posterior femur, 2.6 mm.

Paratypes (2 ♂).

BRAZIL: same data as type, except I-1945, 1 ♂ [A.N.S.P.]; Caviuna, Paraná, X-1946 (Maller), 1 ♂ [A.M.N.H.]

Variation.—The type series varies in size as follows: total body length, 65-68 mm; length of anterior wing, 51-54 mm; length of exposed portion of posterior wing, 6-8 mm. The number of spines on the outer ventral face of the posterior femur varies from 13-17 while those of the inner ventral face vary from 6-9. In other features the type series is quite constant and agrees with the type.

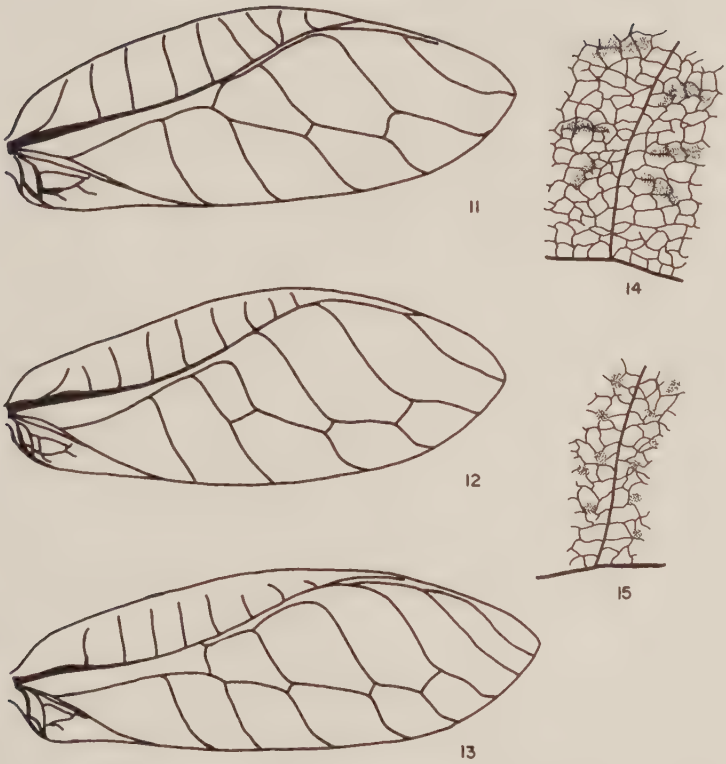
Rossophyllum colosseum (Brunner) new combination Plate XXIII, B

Microcentrum colosseum Brunner, 1878, Monographie der Phaneropteriden, Vienna, p. 341. [Santa Marta, Colombia; ♀.]

Microcentrum colosseum Brunner; Saussure and Pictet, 1898, Biologia Centrali-Americana, Insecta, Orthoptera, I, pp. 362, 363, pl. XVII, figs. 9, 10. [Bugaba, Panama; ♂.]

Through the cooperation of Dr. Max Beier of the Natural History Museum of Vienna, it was possible to establish the identity of this species by comparison of a specimen with the type. The species is redescribed and figured below.

Diagnosis.—This, the smallest known species of the genus, differs from its congeners in possessing posterior femora which are



Figs. 11-15.—Right anterior wings of males of *Rossophyllum*. Fig. 11, *Rossophyllum sentum*, type; Fig. 12, *Rossophyllum clausum*, type; Fig. 13, *Rossophyllum colosseum* (Brunner); Fig. 14, detail showing the pigmented areas located in the archedictyon of the diaphanous bands in the fore wing of *Rossophyllum sentum;* Fig. 15, the same in *Rossophyllum colosseum*.

slightly more robust, these being only 7 times or less longer than broad. Additional differentiating characters are discussed in the diagnoses of the two preceding species.

Male; head.—Similar in form to the preceding species, but much smoother with very few, weak punctures on the vertex only. Dorsum of vertex about .8 times the depth of an eye higher than the dorsal surface of the eyes in lateral aspect. Interocular width of vertex about 3.1 times the width of an eye and about 1.6 times the interantennal width.

Pronotum.—Similar in form to the preceding species, but much smoother with numerous very weak punctures especially on the dorsal surface. Median, dorsal length about 1.3 times the greatest dorsal width. Lateral lobes about 1.5 times deeper (dorso-ventrally) than broad (greatest dimensions).

Wings.—Venation and shape of anterior wing as in fig. 13. Anterior wing about 3 times longer than broad. Posterior wings (when folded) exceeding anterior wings by about one-eighth the length of the latter. Fore wing distally more angulate (fig. 13). Pigmented areas of diaphanous bands of anterior wing as in fig. 15.

Legs.—Anterior femora with 4-5 weak spines along inner ventral face. Posterior femora about 7 times longer than broad; with 12-13 moderately developed spines on outer ventral face; inner ventral border with 6-7 weak spines in distal half only.

Abdomen.—Subgenital plate similar to *R. clausum* (fig. 10). Cerci bearing 2 distal teeth (fig. 6). Tenth abdominal tergite as in preceding species. Supra-anal plate little produced, but lacking the median sulcus (fig. 5).

Measurements.—Total body length, 50-53 mm; median length of pronotum, 6.2-7.1 mm; length of anterior wing, 41-42.5 mm; greatest breadth of anterior wing, 14-15 mm; length of exposed portion of posterior wing, 5-5.9 mm; length of posterior femur, 19.1-20 mm; greatest breadth of posterior femur, 2.7-2.9 mm.

The following description of the female is comparative to that of the male.

Size.—Larger.

Head.—Dorsum of vertex about .9 times the depth of an eye higher than the dorsal surface of the eyes in lateral aspect. Interocular width of vertex about 3.6 times the width of an eye and about 1.5 times the interantennal width.

Wings.—Anterior wing of greater breadth, about 2.3 times longer than broad.

Legs.—Anterior femora with 5 (right) to 6 (left) weak spines along inner ventral face. Posterior femora about 6.7 times longer than broad; with 14-15 moderately developed spines on outer ventral face; inner ventral border with 7 weak spines in distal half only.

Abdomen.—Ovipositor similar in form and shape to *R. clausum* (fig. 9), but with a weakly crenulate distal border on both sets of valves.

Measurements.—Total body length, 60 mm; median length of pronotum, 7.2 mm; length of anterior wing, 47 mm; greatest breadth of anterior wing, 20 mm; length of exposed portion of posterior wing, 5.6 mm; length of posterior femur, 21.6 mm; greatest breadth of posterior femur, 3.2 mm; length of ovipositor, 3.7 mm.

Specimens examined (6 ♂, 1 ♀).

PANAMA: Fort Clayton, Canal Zone, III-1944 (Frick), 1 ♂ [C.A.]; Barro Colorado Island, Canal Zone, 8-II-1955, 15-VI-1956, 18-VI-1956, 10-VII-1956, 13-VIII-1956 (Rettenmeyer), 5 ♂ [A.N.S.P.]; La Chorrera, 23-V-1944 (Frick), 1 ♀ [C.A.].

No significant variation is noted in this series.

REFERENCE

RAGGE, D. M. 1955. The wing-venation of the Orthoptera Saltatoria. London. British Museum (Natural History), 159 pp.

EXPLANATION OF PLATE XXIII

(All figures enlarged)

A. Left lateral aspect of *type—Rossophyllum clausum* n. sp.
B. Left lateral aspect, ♂, Barro Colorado Island, Panama—*Rossophyllum colosseum* (Br.)
C. Left lateral aspect of *type—Rossophyllum sentum* n. sp.

GRANT: GENUS ROSSOPHYLLUM

AN ANALYSIS OF OVIPARITY AND VIVIPARITY IN THE BLATTARIA

BY LOUIS M. ROTH AND EDWIN R. WILLIS

Pioneering Research Division
U. S. Army Quartermaster Research and Engineering Center
Natick, Massachusetts

Various workers have grouped species of Blattaria according to mode of ovipositional behavior and type of oötheca. Holmgren (1903) erected three categories as follows:

1. Oviparous species which carry the oötheca for some days protruding from the end of the abdomen (e.g., *Periplaneta* spp.).
2. Viviparous species which carry the oötheca during embryonic development within a strongly developed uterus.
   a. Species with normally constructed oöthecae (e.g., *Eustegasta micans* Saussure and Zehntner, *Oxyhaloa saussurei* Borg, *Blaberus* sp.). [We presume that by "normally constructed oöthecae" Holmgren meant a relatively thick oöthecal wall as opposed to the thin membrane in "b".]
   b. Species with oötheca reduced to a very thin, practically wanting, membrane (e.g., *Panchlora viridis* (Fabricius)).

Shelford (1906) modified Holmgren's classification as follows:

1. Oviparous species. Eggs enclosed in a chitinous oötheca and carried by the female for a short time only (e.g., *Ectobius, Blatta,* and *Periplaneta* spp.).
2. Ovoviviparous species.
   a. Eggs enclosed in a semi-chitinous capsule and carried by the female, protruding from the abdomen, during the greater part of the embryonic period (e.g., *Blattella germanica* (Linnaeus)).
   b. As above, but eggs enclosed in a transparent membrane (e.g., *Temnopteryx* sp.). [This category was based on Shelford's observation of a single specimen from East Africa. Shelford stated that this female carried the eggs in a transparent membrane protruding from the end of the abdomen, and that the eggs were in a very advanced state of development. Later Shelford (1910) assigned the name *Temnopteryx abyssinica* Saussure and Zehntner to what seems to be the above specimen, and in 1913 he placed *T. abyssinica* in synonymy with *Hemithyrsocera circumcincta* Reiche and Fairmaire; he repeated his earlier observation of the protruding oötheca and stated that the egg case was a thin-walled, membranous sac, carried with the suture directed to one side, and so transparent that the eyes of the contained embryos could be seen

through the walls (true also of the oötheca of *Blattella germanica*). He further added that the egg case was probably deposited only a few hours before emergence of the young and was thoroughly characteristic of the Pseudomopinae. However, in 1912 Shelford grouped *Hemithyrsocera* and *Blattella* together as having leathery oöthecae. Very likely " a " and " b " above are the same category. Rehn (1933) made *Hemithyrsocera circumcincta* the genotype of the new genus *Burchellia*.]

3. Viviparous species.
   a. Eggs enclosed in a chitinous oötheca which is retained in the brood sac of the mother (e.g., *Oxyhaloa saussurei, Eustegasta micans, Blaberus* sp.).
   b. Eggs enclosed in a transparent membrane which is retained in the brood sac of the mother.
      i. Membrane complete (e.g., *Molytria maculata* Brunner, *Epilampra burmeisteri* (Guérin), *Panchlora nivea* (Linnaeus) [=*Panchlora virescens* Thunberg], *Panesthia angustipennis* (Illiger) [=*P. javanica* Serville]).
      ii. Membrane incomplete (e.g., *Panchlora viridis* (Fabricius), *Panchlora nivea*).

Oöthecae do not contain chitin (Campbell, 1929; Tauber, 1934, Pryor, 1940) and by the term " chitinous " Shelford was probably indicating that the oötheca was sclerotic rather than membranous (cf. Torre-Bueno, 1937). The classification of oöthecae into structures which are " complete " or " incomplete " is a dubious one. Hagan (1951) found that the oötheca of *Diploptera punctata* (Eschscholtz) [=*Diploptera dytiscoides* (Serville), Princis (1950)] is never complete even at the time of oviposition; as the embryos grow and the eggs elongate, the oöthecal membrane covers less and less of the egg mass. This also holds true for other species that incubate their eggs internally; in some so-called " ovoviviparous " species the oötheca may be nearly complete or definitely incomplete depending on the age of the eggs at the time the observation was made. In an earlier paper (1954) we stated that the oötheca of *Nauphoeta cinerea* (Olivier) is incomplete. This conclusion was based on oöthecae containing well-developed eggs (Plate XXIX, figs. 44, 45); in one oötheca containing well-developed eggs the membrane covered only 84 percent of the length of the eggs. However, newly formed oöthecae of *N. cinerea* have an oöthecal membrane which covers all of the eggs (Plate XXIX, fig. 43). Pope (1953) stated that

the egg mass of *N. cinerea* is covered by a soft, transparent membrane but that there was no egg capsule; the thin membrane around the eggs actually is the oötheca. In recently formed oöthecae of *Pycnoscelus surinamensis* (Linnaeus) the extent of the oöthecal membrane may vary from specimen to specimen. In some, practically all of the eggs are covered (Plate XXIX, fig. 51); others have a distinct separation along the micropylar region (Plate XXIX, fig. 52); whereas in still others, eggs in the same oötheca may be either completely or only partly covered. The oöthecal membrane of *Leucophaea maderae* (Fabricius) usually extends to within a short distance of the micropyles of the eggs. But we have seen an oötheca of this species in which the membrane covered from 62 to 92 percent of the length of the eggs. Both Riley (1891) and Shelford (1906) differed in their interpretation of the extent to which the eggs are covered by the oötheca of *Panchlora* (Plate XXIX, figs. 49-50), although it is clear that both were probably dealing with the same or very similar species (Roth and Willis, 1957a). In fact Shelford (1912) in his diagram showing the possible evolution of viviparity listed *Panchlora* as possessing no oötheca.

Roth and Willis (1954, 1955b) suggested the following classification:

1. Oötheca extruded, not rotated, carried by the female for only a short time, then deposited, and abandoned (e.g., *Periplaneta americana* (Linnaeus), *Blatta orientalis* Linnaeus, *Eurycotis floridana* (Walker), *Supella supellectilium* (Serville)).

2. Oötheca extruded, rotated, carried by female for a longer period of time than in the first category, but eventually deposited a long time before hatching (e.g., *Ectobius panzeri* Stephens).

3. Oötheca extruded, rotated, carried by female until, or shortly before, hatching (e.g., *Blattella germanica, Blattella vaga* Hebard, *Blattella humbertiana* (Saussure)).

4. Oötheca extruded, rotated, and retracted into a brood sac where the embryos develop until, or shortly before, hatching (e.g., *Nauphoeta cinerea, Pycnoscelus surinamensis, Leucophaea maderae, Blaberus craniifer* Burmeister, *Gromphadorhina laevigata* Saussure and Zehntner).

5. Oötheca possibly not extruded; the eggs probably directed from the oviducts into the brood sac where they remain until hatching (e.g., *Diploptera punctata*). [This category does not exist because we (1955c) have since shown that the oviposition behavior of *Diploptera* is similar to that of the "ovoviviparous" species of category 4.]

The length of time the female of any one species carries the oötheca may be subject to some variation, possibly as a result of environmental differences. *Blatta orientalis* (Plate XXIV) has been claimed to form and drop its oötheca in from 12 hours (Moore, 1900) to a week or more (Miall and Denny, 1886; Blatchley, 1920). Rolander (in Roth and Willis, 1955b) claimed that *Ectobius pallidus* (Olivier) [=*Ectobius livens* (Turton)] carried its oötheca up to 16 days or longer before depositing it, whereas we (1957) found that the female formed and deposited its oötheca within one or two days in the laboratory. *Supella supellectilium* usually carries its oötheca from 24 to 50 hours, but at low temperatures this period may be prolonged for several days (Hafez and Afifi, 1956). Pope (1953) also noted that *Supella* at times carried its oötheca up to 8 days before depositing it.

One of the earliest records of cockroach viviparity was the observation of a female expelling well-developed embryos from her genital tract after she had been dropped into alcohol (Robert, 1836). Viviparity has been defined as the birth of offspring without an enveloping egg shell, whereas oviparity was stated to be the extrusion of eggs or offspring that are surrounded at birth by a chorion (Hagan, 1948). The difficulty in using the above definitions for devising a classification for cockroach viviparity results from the conflicting concepts that " ovoviviparous " cockroaches have two birth products, the egg and the nymph. We now know that all cockroaches whose oviposition behavior has been observed extrude their oöthecae, during formation, outside the female's body (Plates XXIV; XXV; XXVIII, fig. 38); the " ovoviviparous " and " viviparous " species then retract or deposit the egg case into a brood sac or uterus (Plate XXV, figs. 13-20); this behavior was first described by Chopard (1950) in *Gromphadorhina laevigata*. The initial behavior of extruding eggs in the oötheca satisfies the criterion for oviparity, and from a behavioral veiwpoint all cockroaches are, as far as we know, in this sense oviparous. The term viviparity has been generally accepted by entomologists to mean the birth of young in some pre-adult stage other than the egg, and oviparity the deposition of eggs that subsequently hatch into one of the pre-adult stages (Hagan, 1931).

Hagan (personal communication) believes that the extrusion of the oötheca is truly oviposition; the eggs are secondarily deposited by retraction of the oötheca into the brood sac for further maternal care. This subsequent disposition of the oötheca in the female's brood sac does not make the female viviparous when the nymphs are born. For this reason, we (1955b) called the behavior of extruding and retracting the oötheca (Plate XXV, figs. 13-20) false ovoviviparity and stated further: "True ovoviviparity would encompass those animals in which eggs, with enough yolk to allow the embryos to complete development, are retained within the female's body from formation until hatching. We know of no truly ovoviviparous cockroaches at this time." Although other workers have stated that the eggs of certain species of cockroaches are "retained in a brood sac", they were not cognizant of the complete ovipositional behavior of these species which first extrude their oöthecae and then retract them into the body; by *retained* we mean that the newly formed eggs are never extruded but remain within the female's body at all times.

While developing in the brood sac the eggs increase greatly in size and may split their egg membranes and grow out of the oötheca to some extent. In an earlier publication (1954) we stated that presumably hatching of the eggs does not occur within the brood sac because the embryos are too tightly invested by the uterus; by hatching we had in mind complete escape of the embryo from its egg membranes. However, if one considers hatching as the breaking of the egg-shell by the insect in the process of emerging, as it has been defined by Torre-Bueno (1937), then hatching (or at least partial hatching) of some of these brood-sac species may be said to have taken place in the uterus (Plate XXIX, figs. 44, 45). But this splitting of the egg membranes may occur some time before the matured embryos are extruded by the mother. That is, the egg membranes do not suddenly break at the time of birth but some time earlier during the process of growth and before the embryos are capable of completing hatching or of independent life; the splitting is probably a gradual process following the increase in the size of the eggs. Although the egg membranes may have been broken while the eggs were still in the uterus, the embryos are not completely free

but are partly enclosed by the oötheca and embryonic membranes which still invest them as they are extruded by the female (Plate XXVIII, figs. 40-42).

According to Holmgren (1903) in *Eustegasta* the oötheca ruptured in the mother, and the nymphs hatched by twos. Shelford (1912) interpreted Holmgren's remarks to mean that the ". . . capsule splits open inside the brood sac allowing the young to escape before the oötheca itself is actualy got rid of." It is likely that the parturient behavior of *Eustegasta* is no different from *Blaberus* or *Nauphoeta* or any other " ovoviviparous " cockroach in which the young escape as the oötheca is re-extruded by the female (Plate XXVIII, figs. 39-42). Shelford placed *Eustegasta* in the same class as *Blaberus* and stated that they both have " chitinous " oöthecae. In *Blaberus craniifer,* at the time of oviposition the oötheca covers almost all of the eggs, only the micropylar areas being exposed. While removing from a female an oötheca containing fully developed eggs (which then began to hatch), we found that the oötheca covered only about the lower half or less of the embryos. These embryos had not only " grown out " of their oöthecal covering but were almost entirely free of their embryonic membranes which remained in the oötheca after the young walked away.

The extent to which the embryos are free of membranes at the time of extrusion by the female seems to depend on the extent to which the eggs were initially covered by the oötheca at its formation and the amount of increase in size of the egg that takes place during embryogenesis (see above). Thus in *Diploptera* the oötheca at the time of formation (Plate XXIX, figs. 53-54) covers considerably less of the eggs than do the oöthecae of the " ovoviviparous " species. The eggs of *Diploptera* increase in length more than 7 times by the time the embryos are ready to be born, and at parturition only a very small part of the embryos are covered by either oötheca or embryonic membranes. As the young of *Diploptera* are extruded they are essentially free from embryonic covering and oötheca (Plate XXVIII, fig. 39), and in this species this final birth product may be said to fullfill a criterion for viviparity; even in this species the remnant of the oötheca is extruded after parturition. The second birth product

of the brood-sac species is generally a completely developed embryo which may be more or less covered by oöthcal and embryonic membranes (Plate XXVIII, figs. 40-42). The first birth product, of course, is the egg which is extruded when the female forms the oötheca.

Hagan (1951) subdivided viviparous species of insects into four general classes based upon modifications *possibly* concerned with the manner of nourishing the embryos in the mother. The following two of his four categories could apply to cockroaches:

1. Ovoviviparity. The egg contains sufficient yolk to nourish the embryo until hatching and maternal deposition of offspring. No special nutritional structures are developed. [In his Table 6 on page 61, Hagan (1951) lists as examples of this category, *Blatta, Blaberus, Eustegasta*, etc. Undoubtedly the inclusion of *Blatta* was a lapsus calami as this is strictly an oviparous genus.]
2. Pseudoplacental viviparity. The embryo in the maternal genital tract obtains at least part of its nutriment by means of a pseudoplacenta which, in the free-embryo type, is wholly of embryonic origin. Contact of egg, pseudoplacenta, or embryo with the maternal genital tract is maintained only by pressure or proximity (e.g., *Diploptera punctata*).

Hagan (1939, 1951) suggested that the pleuropodia may be the pseudoplacenta in *Diploptera*. The function of the pleuropodia in cockroaches is still unknown even though Hagan (1939, 1951) tentatively ascribed to them nutritional or respiratory functions, or both. It should be pointed out that the " ovoviviparous " species also have pleuropodia (Plate XXX) which in some species (e.g., *Leucophaea maderae* and *Nauphoeta cinerea*) have greatly elongated extensions. Stemley (1956) has described the pleuropodia in *Nauphoeta cinerea*. The pleuropodia of *Blaberus craniifer*, *Byrsotria fumigata*, and *Pycnoscelus surinamensis* apparently lack elongated extensions, at least in the stages shown in Plate XXX. Even the oviparous species such as *Blatta orientalis* and *Blattella germanica* have pleuropodia (Wheeler, 1890; see Hussey, 1926, for a review of pleuropodia in insects). Even if there is a relationship between the pleuropodia and the mother in the " ovoviviparous " species, a similar relationship does not exist in those species in which the eggs develop away from the body of the female.

From a study of the water relationships in the eggs of cockroaches with different oviposition behaviors one significant similarity stands out; during embryogenesis the eggs of all the species thus far investigated gain water as they mature (Roth and Willis, 1955, 1955a-c). Possibly the pleuropodia operate in the uptake of water by the eggs of all species and may even function in the intra-uterine nutrition of *Diploptera* whose eggs increase in dry weight as well as water. Hagan (1948) stated that pseudoplacental viviparity may merely employ in a different way structures commonly present in ovoviviparous species. The pleuropodia have different forms in different species of cockroaches, but they may or may not function alike in all species. Until the functions of the pleuropodia are determined, we can only speculate on their significance in devising a classification of viviparity in cockroaches.

With the exception of Hagan's (1951) classification practically all of the previously described classifications of cockroach viviparity have been based on the ovipositional behavior of the female, the type of oötheca formed, and whether or not the eggs were found in a brood sac. The nutrition of the embryo after the eggs have been deposited (whether deposited away from or within the female) has been ignored probably because little was known about the embryonic nutrition of cockroaches. We now know that one of the consistent similarities in all species of cockroaches studied is the uptake of water during embryogenesis, although the source of this water varies with differences in ovipositional behavior. Another important aspect of cockroach embryogenesis is whether or not the eggs increase in dry weight. At present only one species of Blattaria, *Diploptera punctata*, is known in which the developing eggs increase in dry weight. It was this, as well as the observation that during oöthecal formation most of the eggs are not extruded beyond the abdomen of the female that led us to state (1955c) that *Diploptera* may be the only known case of true viviparity among cockroaches. However, we can not ignore the method of the formation of the oötheca by *Diploptera* which is the same as that in the oviparous and " ovoviviparous " cockroaches; most of the eggs of *Diploptera* are not seen at the time of oviposition (Plate XXVIII, fig. 38) because they are small in size and few in number and are thus concealed by the genital

chamber before being retracted into the brood sac. Concerning the development of viviparity in cockroaches, Hagan (personal communication) wrote: " No doubt evolution is progressing at a slow rate toward viviparity, I should judge, and the oötheca will be retained in the brood sac from the very first if this series of steps was complete. Such an event may require a reduction in the number of ovarioles and eggs in a clutch so the genital chamber may accommodate them without their temporary protrusion." From a behavioral point of view *Diploptera punctata* is a false ovoviviparous genus, but its embryonic nutrition differs markedly from the other species in this category.

Hagan (1931) has stated: " The fact that an insect deposits its young in the form of larvae or eggs is a point of secondary importance. In other words, the hatching of the eggs within the maternal uterus or after deposition is simply a physical phenomenon of slight significance unless it be due to structural changes or physiological readjustments on the part of the mother or offspring, or both." As we have pointed out, the physiological mechanism by which the embryos gain water or water and solids are still unknown. As for the respective reproductive systems, the " viviparous " *Diploptera* possesses no new structures when compared with the oviparous *Blatta;* the reproductive systems of the two genera possess similar subdivisions which vary only in their shapes, relative sizes, and functions (Hagan, 1941).

From our earlier studies on cockroach eggs (Roth and Willis, 1954, 1955, 1955a-c, 1957, 1957a) and with the preceding discussion in mind, we suggest the following classification of oviparity and viviparity in the Blattaria.

I. Oviparity. Eggs develop outside the body of the female.
   1. The oötheca is carried by the female for various periods of time (usually 24 hours or more) but is eventually deposited long before the eggs hatch (Plate XXVI).
      a. At the time of oviposition the oötheca and eggs do not contain sufficient moisture for the eggs to develop. The oötheca is deposited by the female in a humid or moist environment where, sometime during embryogenesis, the eggs absorb moisture through the oötheca (which generally swells markedly) from the moist substrate. In a comparatively dry atmosphere the oötheca is unable to retain water and the eggs will dry out (e.g.,

Ectobius pallidus, Cariblatta lutea minima Hebard, *Parcoblatta virginica* (Brunner)). It is possible that this category should be subdivided into species in which the eggs seem to undergo diapause (e.g., *Ectobius pallidus*) or have an initial low or high water content. The oöthecae and eggs of *E. pallidus* at the time of oviposition contain an average of 40 percent water, whereas those of *Parcoblatta virginica* contain 57 percent water when deposited.

b. At the time of oviposition the oötheca and eggs contain sufficient moisture for the eggs to develop without obtaining water from the environment outside the oötheca. The eggs take up water from the interior of the oötheca during embryogenesis.[1] The oötheca possesses a protective layer which retards water loss, and the eggs are able to develop independent of a high humidity or a moist substrate. The water content of oöthecae and eggs at the time of oviposition averages about 60 to 64 per cent (e.g., *Blatta orientalis, Periplaneta americana, Supella supellectilium*).

2. Oötheca carried externally (Plate XXV, figs. 7-12) by the female until or shortly before the young hatch (Plate XXVII). The end of the oötheca which is held by the female is permeable to water, and the embryos derive water, in addition to that originally present in the eggs, from the female. The free or exposed end of the oötheca is relatively impermeable to water and thus retards loss of water from the eggs (e.g., *Blattella germanica, Blattella vaga*, and probably other species of *Blattella* such as *B. lituricollis* (Walker) and *B. humbertiana* which carry the oötheca until the eggs hatch.) The water content of the oöthecae at oviposition in *B. germanica* averages 62 percent and in *B. vaga* 60 per cent.

II. False Ovoviviparity. Eggs develop in a brood sac or uterus inside the body of the female. The formation of the oötheca is the same as in the oviparous species and practically all of the eggs are extruded beyond the body of the female at oviposition (Plate XXV, figs. 13-20). Once the oötheca has been formed it is retracted into a brood sac, and the eggs are no longer visible from the outside. The oötheca itself is transparent and flexible, varies in thickness, and covers the eggs to a varying degree depending on the species and subsequent state of development of the eggs. At parturition the oötheca is re-extruded and the hatching nymphs drop free from their embryonic membranes

[1] Although water is absorbed by the eggs during embryogenesis, the weight of the oötheca decreases with age because carbon dioxide and some water are transpired. The gross loss of weight by the oötheca does not necessarily indicate loss of water by the eggs; this relationship must be borne in mind when interpreting data on loss of water by oöthecae during incubation as reported for *Periplaneta picea* Shiraki (Yoshikawa and Ikushima, 1956) (cf. *Blatta orientalis* in Roth and Willis, 1955b).

which generally remain in the oötheca (Plate XXVIII, figs. 40-42). The eggs (usually more than 25 in an oötheca) are supplied with sufficient yolk to enable the embryos to complete development; the embryos absorb only water from the female and lose dry weight during embryogenesis. At formation, the water content of the oöthecae and eggs averages 34 to 40 percent.

1. Oötheca thick (at formation) and distinctly dark in color (e.g., species of Blaberinae[2] such as *Blaberus craniifer, Blaberus giganteus* (Linnaeus), and *Byrsotria fumigata*).
2. Oötheca relatively thinner than in No. 1 and varying from colorless to yellowish or amber colored (e.g., species of Epilamprinae[2] such as *Nauphoeta cinerea, Leucophaea maderae, Pycnoscelus surinamensis* and *Panchlora nivea*).

Most of the species of cockroaches that have previously been considered in the literature to be ovoviviparous and that produce an oötheca containing 25 eggs or more would probably belong to category II.

III. False Viviparity. The oötheca is formed and the eggs deposited in a manner similar to that in the false ovoviviparous species (category II). The developing eggs absorb not only water but solids from the female and increase markedly in dry weight. The newly formed oöthecal membrane is very thin and greatly reduced; it surrounds only the basal halves of the eggs. There are on the average about 12 very small eggs only one or two of which protrude beyond the female's abdomen during oviposition (Plate XXVIII, fig. 38). *Diploptera punctata* is the only known example, but it is probable that other species with similar ovipositional behavior and which produce a comparatively small number of eggs belong in this category. The eggs initially contain about 34 percent water.

Actually, color is not a very good character for separating the oöthecae of the Blaberinae from those of the Epilamprinae (category II above). For one thing, the color of the oötheca of the same egg mass may vary from one region to another depending on the thickness of the oöthecal membrane. Also the oöthecae are more or less transparent so that the color of the eggs will influence an evaluation of the color of the egg case. We have examined against a white background pieces of moist oöthecae removed from around the eggs of several species. Though the oötheca of *Blaberus craniifer* is the darkest amber colored of the four species observed in this way, the oöthecae of *Pycnoscelus*

[2] Taxonomic classification of J. W. H. Rehn (1951).

surinamensis and *Leucophaea maderae* are distinctly yellowish amber. The oötheca of *Nauphoeta cinerea* which is almost colorless has a yellowish cast when viewed under the microscope. It would not be difficult to arrange a graded series of oöthecae from the thick, darkly colored oötheca of *Blaberus* to very thin, practically colorless oöthecae of *Nauphoeta* and *Panchlora.*

The different oöthecae of the Blaberinae and Epilamprinae (Plate XXIX, figs. 43-52) possibly represent stages in the evolution of " viviparity " in blattids, although we do not mean to imply that one gave rise to the other. Holmgren (1903) believed that the evolution of " viviparity " in cockroaches could be traced from *Periplaneta* through the intermediate stage of *Blaberus* to its maximum development in *Panchlora;* today *Diploptera* would be considered the most highly evolved. Shelford (1912) suggested that the *Panchlora* type of oötheca may have been derived from a *Eustegasta* type (a category which includes *Blaberus*) or from the kind of oötheca found in *Blattella germanica.* He favored the idea that the *Blaberus* type evolved from the *Blatta* type. However, it is just as logical to suppose that the *Blaberus* type evolved from the *Blattella*-like oötheca; the *Blaberus* oötheca is more like that of *Blattella* in appearance and texture than that of *Blatta.* In an earlier paper (1955b) we suggested that in the evolution of " viviparity ", the behavior may have evolved from species that dropped their egg cases (*Periplaneta,* etc.) to females that carried the eggs externally until they hatched (*Blattella*) to females that retracted their egg cases into a brood sac within the body (*Nauphoeta, Leucophaea, Blaberus,* etc.). Once the egg case could be safely housed in a uterus, degeneration of the oötheca could occur without destruction of the eggs by dehydration. Thus the oötheca of *Blaberus* may represent a stage in degeneration which eventually leads to the very thin membranes characteristic of *Nauphoeta, Panchlora,* and *Diploptera.* Ultimate " viviparity " appeared when solid nutriment (in addition to yolk in the eggs) as well as water were supplied by the mother to the developing embryos (*Diploptera*).

Hagan (personal communication) has stated: " I have come to the conclusion one must be either a ' lumper ' or a ' splitter ' in the matter of classification of insect viviparity. If the latter view is

favored the case is well nigh hopeless, for such a multitude of insects are border line cases that a full taxonomic key would quickly become necessary and one would find no correlation whatever between allied species in it." It is not our intention to add to the general confusion of the classification of insect viviparity. However, we feel that the reproductive habits of cockroaches that incubate their eggs in a brood sac are special cases which, when they are compared with the ovipositional behavior of other cockroaches and placed in the proper perspective, fit into a logical and orderly system.

Summary

Earlier classifications of oviparity and viviparity in Blattaria are discussed. The following new classification, based on ovipositional behavior of the females and on water and dry matter relationships of the eggs during embryogenesis, is suggested.

I. Oviparity. Eggs develop outside the body of the female.
   1. Oötheca deposited long before the eggs hatch.
      a. At oviposition the oötheca and eggs do not contain sufficient water for embryogenesis. The oötheca is deposited in a humid environment and water is absorbed through the oötheca from the substrate. In a dry environment water is lost and the eggs desiccate. (*Ectobius pallidus, Cariblatta lutea minima, Parcoblatta virginica.*)
      b. At oviposition the oötheca and eggs contain sufficient water for the eggs to develop. The oötheca is capable of retarding water loss and the eggs can develop at relatively low humidities. Water is taken up by the eggs from inside the oötheca during embryogenesis. (*Blatta orientalis, Periplaneta americana, Supella supellectilium.*)
   2. Oötheca carried externally by the female until or shortly before the young hatch; embryos derive additional water from the female. (*Blattella germanica* and *Blattella vaga.*)

II. False Ovoviviparity. Eggs develop inside the body of the female. The oötheca, which usually contains 25 eggs or more, is formed as in the oviparous species but is then retracted into a brood sac. The eggs contain sufficient yolk to complete development; they absorb only water from the female and lose dry weight during embryogenesis.
   1. Oötheca is thick and dark colored. (*Blaberus craniifer, Blaberus giganteus, Byrsotria fumigata.*)

2. Oötheca is relatively thin and varies from practically colorless to yellowish or amber. (*Nauphoeta cinerea, Leucophaea maderae, Pycnoscelus surinamensis, Panchlora nivea.*)

III. False Viviparity. Formation of oötheca and its deposition in a brood sac are similar to the false ovoviviparous species (category II). Eggs, about 12 in number, gain both water and solids from female during embryogenesis. (*Diploptera punctata.*)

Acknowledgments

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Explanation of Figures

Plate XXIV

Blatta orientalis forming an oötheca. (× 1.2.)

Fig. 1, Start, 0 hours. Fig. 2, 1 hour. Fig. 3, 2 hours. Fig. 4, 4 hours. Fig. 5, 6 hours. Fig. 6, 8 hours (oötheca nearly complete).

Plate XXV

Oötheca formation in *Blattella germanica* and *Nauphoeta cinerea.*

Figs. 7-12, Oötheca formation in two females of *Blattella germanica.* (× 2.3.)

Fig. 7., Oötheca being formed and extruded with keel dorsad. Figures 8 and 9 were taken 4 and 7 hours respectively after figure 7. The tips of the wings of this female were removed to reveal the oötheca which otherwise would be hidden in dorsal view. Figs. 10-12, fully extruded oötheca being rotated, keel to the right. Figures 11 and 12 were taken 2 and 4 hours respectively after figure 10. The wings were completely removed from this second female to show the contracted abdomen.

Figs. 13-20, *Nauphoeta cinerea* forming and retracting an oötheca. About half the eggs had been laid before the female was seen. (Approximately × 1.7.) Fig. 13, Start, 0 minutes. Fig. 14, 40 minutes. Fig. 15, 1 hour, 10 minutes. Fig. 16, 1 hour, 25 minutes (oötheca beginning to rotate). Fig. 17, 1 hour, 30 minutes. Fig. 18, 2 hours (oötheca rotated and being retracted). Fig. 19, 2 hours, 15 minutes. Fig. 20, 2 hours, 45 minutes (oötheca almost completely retracted).

Plate XXVI

Hatching of eggs of *Periplaneta americana.* (× 1.5.)

Figs. 21-27, Photographs taken at 1-minute intervals. Fig. 28, 20 minutes after figure 21. Note embryonic membranes (arrows) left behind in oötheca.

Plate XXVII

Hatching of eggs of *Blattella germanica.* The oötheca was still held by the female when the eggs began to hatch. The female's wings had been clipped to expose the oötheca. (× 2.5)

Figs. 29-35, Photographs that were taken within a 10-minute period. Fig. 36, 12 minutes after figure 29. Fig. 37, 20 minutes after figure 29. After the eggs had hatched the female dropped the oötheca which was empty except for a number of unhatched eggs.

Plate XXVIII

Oviposition and parturition in *Diploptera,* and parturition in *Nauphoeta.*

Figs. 38-39, *Diploptera punctata.* (× 2.6.) Fig. 38, female ovipositing. Note the two small eggs protruding from end of the abdomen prior to the

oötheca being retracted into the brood sac. Fig. 39, female giving birth. Note the disproportionately large nymphs compared to the small eggs, a result of intra-uterine nutrition.

Figs. 40-42, *Nauphoeta cinerea* giving birth. (×1.7.). The oötheca containing fully developed embryos is being extruded, the embryos dropping free while the anterior end of the egg case is still held in the brood sac of the female.

PLATE XXIX

Eggs and oöthecae of cockroaches that incubate their eggs in a brood sac. The oöthecae were manually removed from the females.

Figs. 43-45, *Nauphoeta cinerea*. (×5.) Fig. 43, Dorsal view of 14-day old oötheca. Note complete oöthecal membrane; the micropyles of several eggs in the lower row show through the transparent membrane. Fig. 44, Dorsal view of 31-day old oötheca. Note well-developed embryos with eye spots; the oötheca, chorions, and embryonic membranes have split freeing the heads of the embryos. Fig. 45, Embryos beginning to emerge from oötheca that had just been removed from female. Note the thin oöthecal membrane and the three embryos that are abnormally positioned with their venters facing outward; the mandibles of these three embryos are visible.

Figs. 46-47, *Blaberus giganteus*. (×2.1.) Fig. 46, Lateral view of oötheca; the first-laid eggs are on the left. Fig. 47, Dorsal view; the incomplete oöthecal membrane does not cover the micropylar ends of the eggs.

Fig. 48, Oötheca of *Blaberus craniifer* from which the young have hatched leaving behind their embryonic membranes. (Lateral view: ×2.1.)

Figs. 49-50, *Panchlora nivea*. (×5.) Fig. 49, Oötheca containing 49 eggs. Fig. 50, Oöthecal membrane separated from eggs by placing the egg mass in KOH.

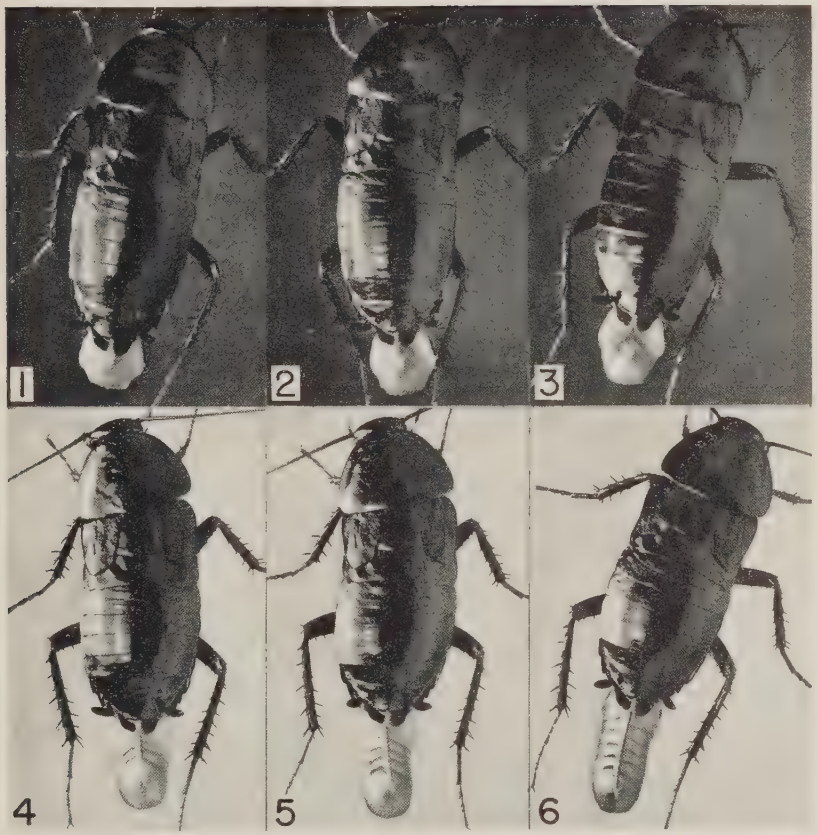
Figs. 51-52, *Pycnoscelus surinamensis*. (×5.) Fig. 51, The oöthecal membrane very nearly covers the apical ends of the eggs. Fig. 52, There is a comparatively wide space between the two lateral edges of the oötheca.

Figs. 53-54, *Diploptera punctata*. (×8.5.) Fig. 53, Oötheca, only a few days old, stained in ferric chloride/potassium ferricyanide. The last-laid eggs are on the left. Fig. 54, Oötheca from which the eggs had been removed in ringer's solution. The last-formed part of the oötheca is on the right.

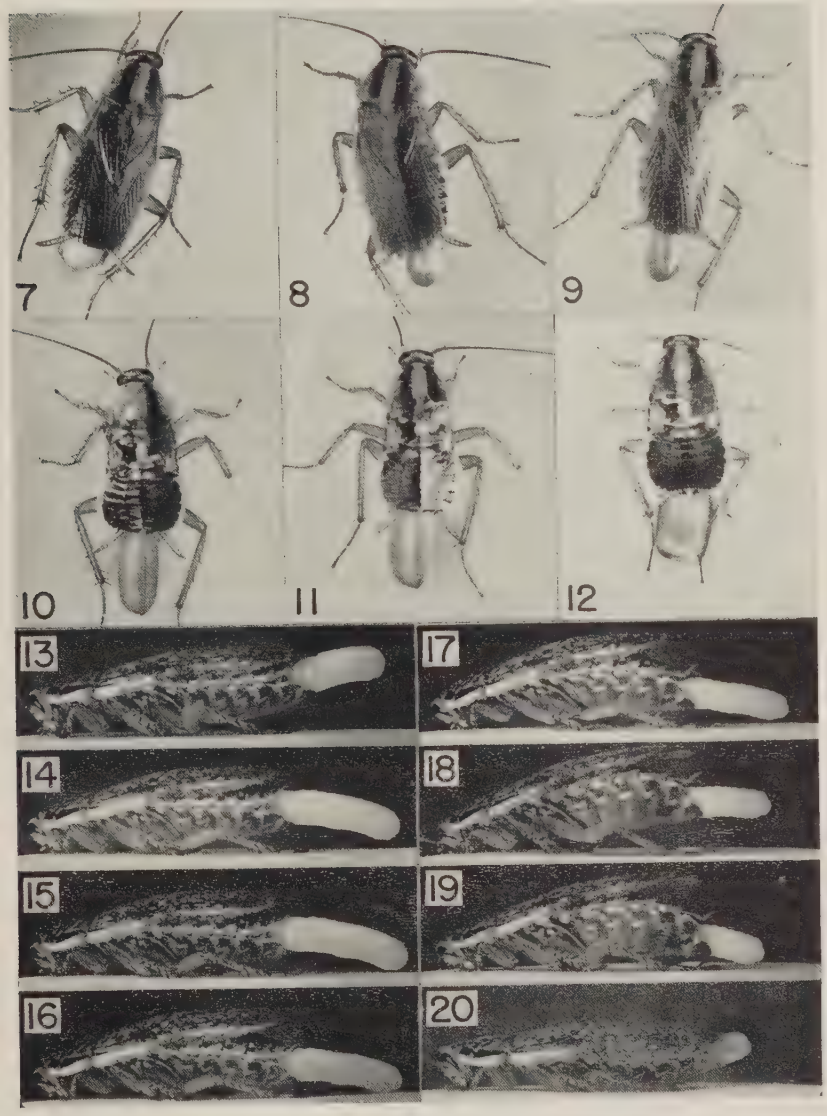
PLATE XXX

Cockroach embryos showing pleuropodia (arrows). The pleuropodia were stained in Nadi reagent. (×13.8.)

Fig. 55, *Leucophaea maderae*. Fig. 56, *Blaberus craniifer*. Fig. 57, *Pycnoscelus surinamensis*. Fig. 58, *Nauphoeta cinerea*. Fig. 59, *Diploptera punctata*.



ROTH AND WILLIS: OVIPARITY AND VIVIPARITY



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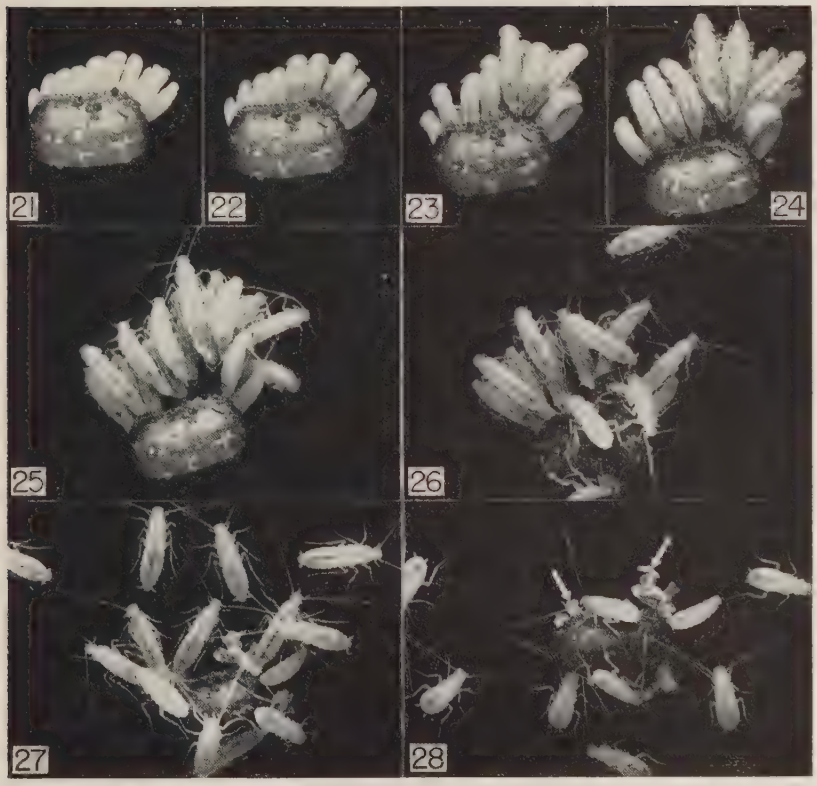

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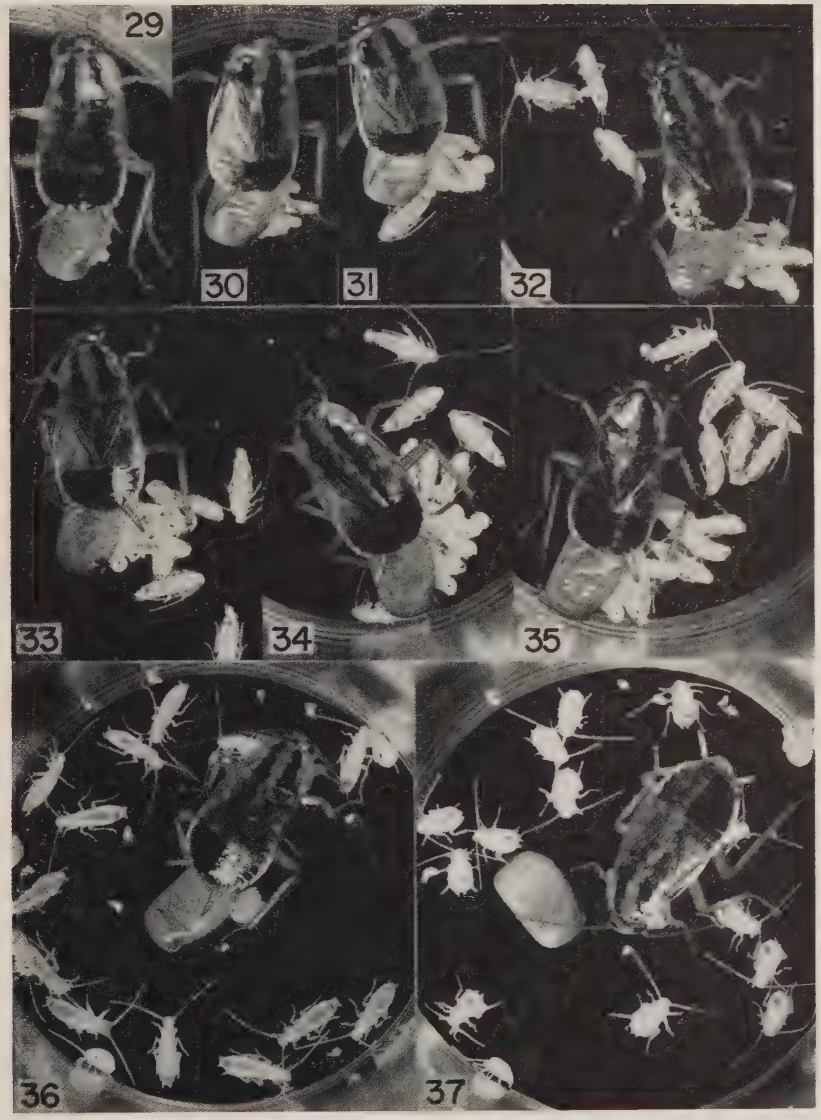

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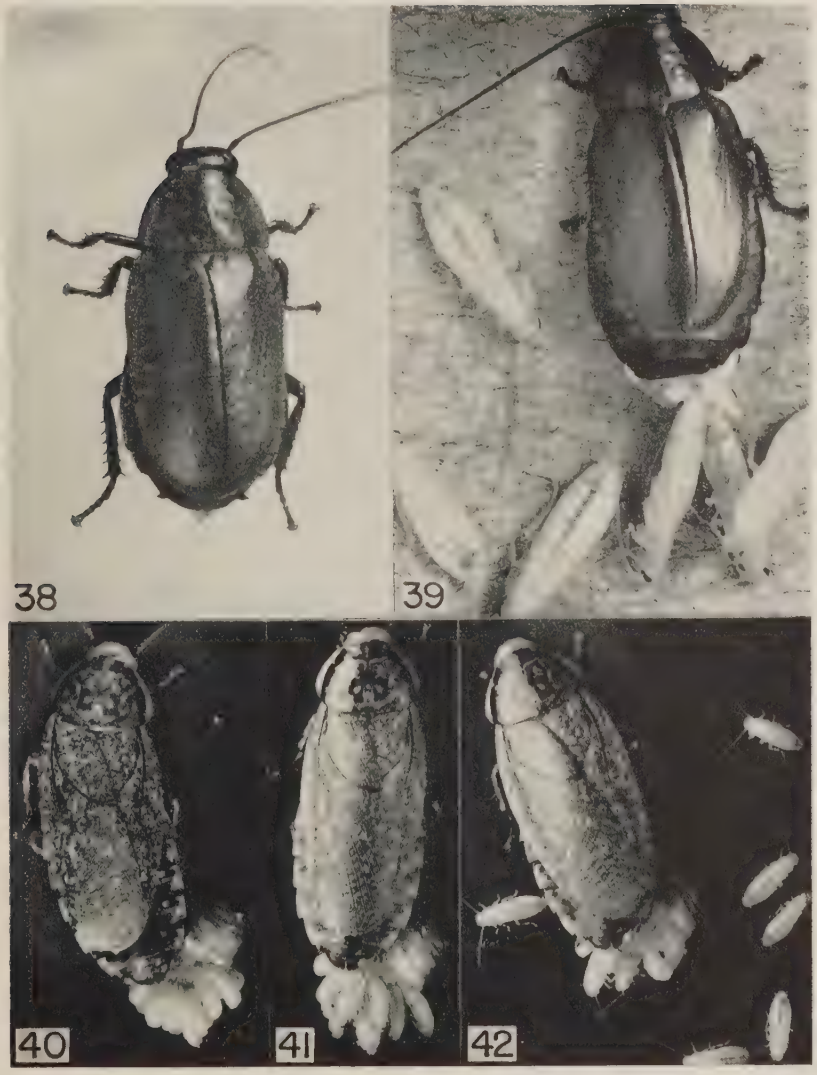

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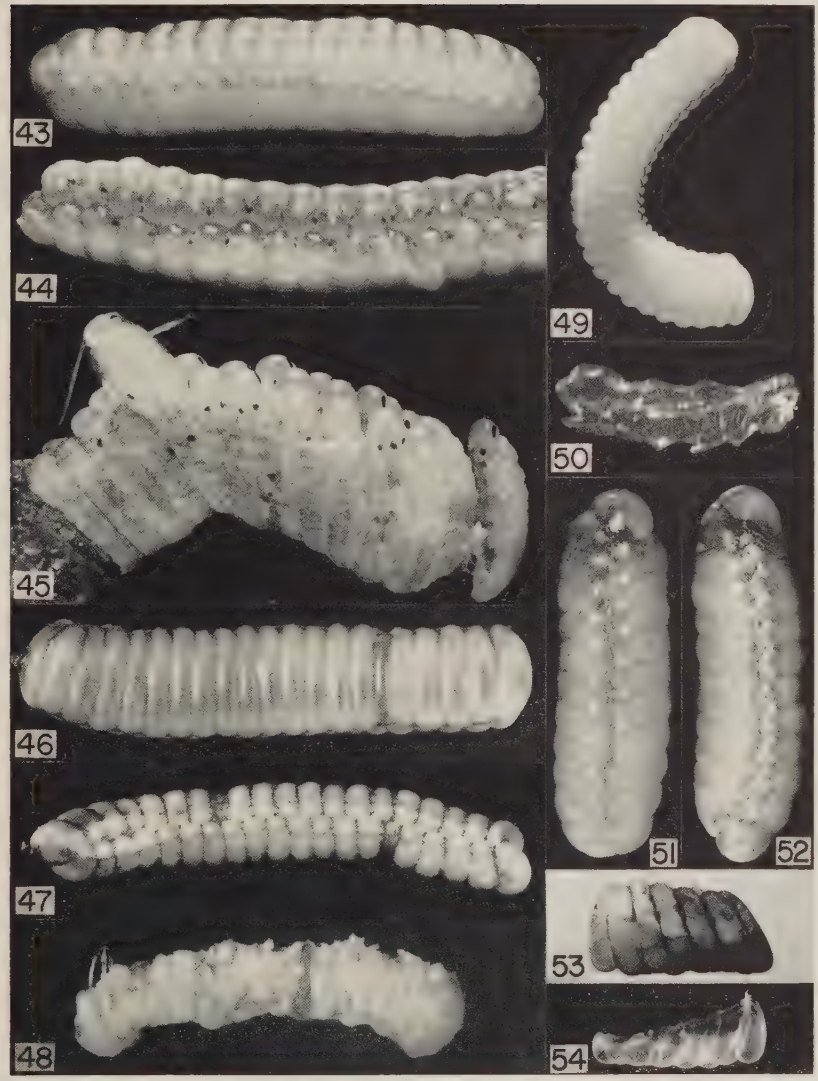

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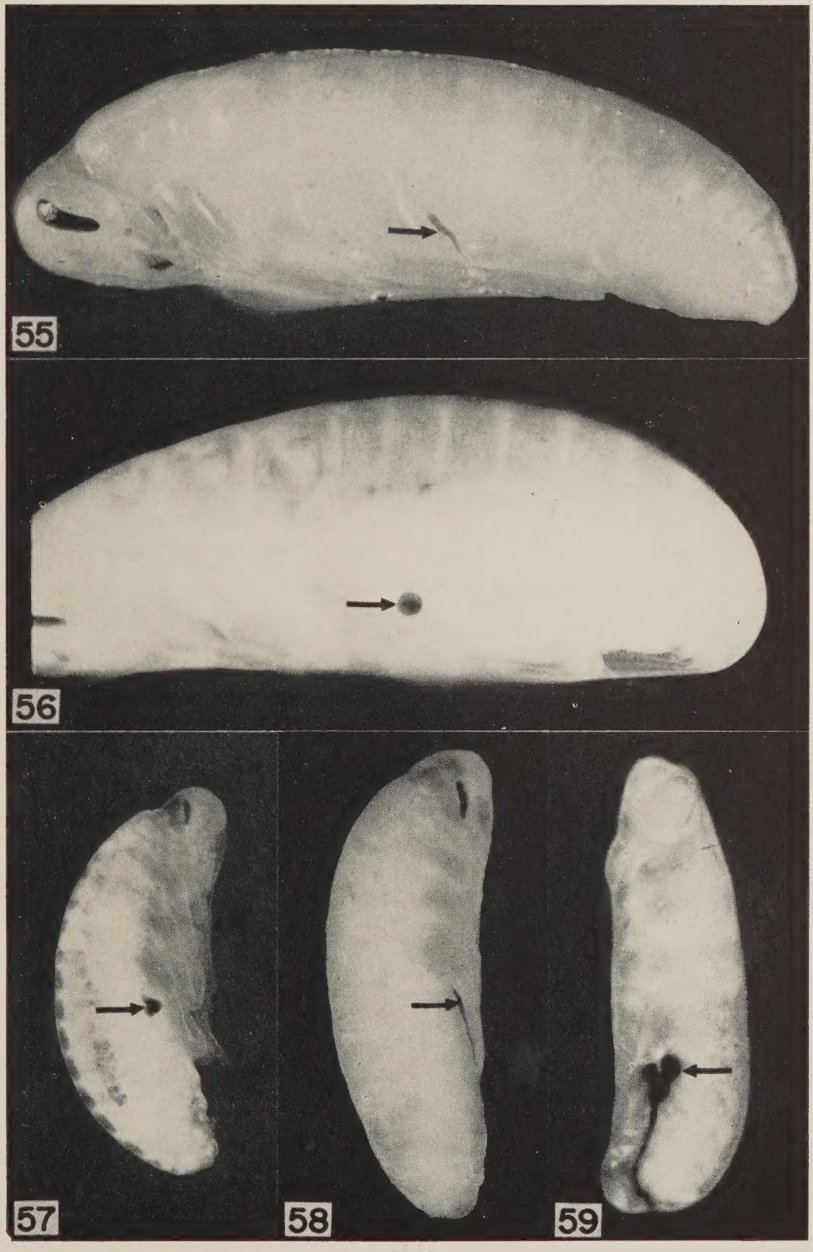

ROTH AND WILLIS: OVIPARITY AND VIVIPARITY

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